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STUDIES ON THE REPRODUCTIVE ORGANS OF THE HETEROPTERA WITH A CONSIDERATION OF THEIR BEARING ON CLASSIFICATION.

By J. G. Pendergrast.

*(Department of Zoology, Auckland University College, New Zealand.)**

Manuscript received 4th June, 1956.

(Read 5th December, 1956.)

With 122 Text-figures.

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I. Introduction, Acknowledgments and Technique.

The aim of this investigation has been to accumulate information on the morphology of the reproductive organs in as large a range of families of the Heteroptera as possible, in order to attempt to estimate the value of the reproductive organs as characters in systematics.

In the females it was found that there is, in general, little diversity in the form of the organs except the spermatheca. Therefore the work in this sex has been concerned, in the main, with this organ. It has a cuticular lining which retains its form in dried specimens. This has enabled the writer to study it in a larger number of families than was possible with the male organs, which have to be examined in fresh or suitably fixed material. A body of pure anatomical and histological information has been collected from these studies, especially in regard to the male organs, but, as much of it is not of direct value in considering the bearing of the organs on classification, it will not be included in the present paper.

* The greater part of the work described here was carried out in the Department of Zoology and Applied Entomology, Imperial College of Science, London.

The writer would like to stress that the study is not an attempt to base a new system of classification on one set of characters. It is realised that an adequate classification of the Heteroptera will be possible only after many characters have been studied in detail throughout the suborder. This study can be regarded only as a preliminary investigation in this field. It will be necessary to examine many more representatives from each group before an adequate appraisal of the value of the reproductive organs in the classification of the Heteroptera can be made.

The reproductive organs were studied by dissection of fresh or fixed material. Bouin's fluid was found to be the most useful fixative because it is often possible to carry out adequate dissections on material treated with it and it also serves as a good general fixative for sectioning. Sections were prepared by ordinary paraffin imbedding, double imbedding with celloidin or by the methyl benzoate-celloidin method. The spermathecae from fresh or preserved specimens were dehydrated, cleared and mounted in balsam. This treatment did not remove epithelia and muscle tissue. Spermathecae from dried material were examined after the abdomen had been boiled in ten per cent. caustic potash and the organ dissected out, stained and mounted in the usual way.

The writer desires to express his gratitude to Professor O. W. Richards, his supervisor, for guidance and criticism ; and to Mr. R. G. Davies for helpful suggestions and advice. His thanks are also due to the authorities of the British Museum (Natural History) for the loan of specimens, and especially to Dr. W. E. China for ready assistance at all times. The writer had many valuable discussions on points of classification with Mr. Dennis Leston, who also generously donated many specimens from his collection.

He would also gratefully acknowledge the help of the following, mainly in providing material for study : Dr. G. L. Arora, Punjab, India ; Dr. J. Carayon, Paris ; Mr. A. J. P. Goodchild, London ; Mr. G. H. Caswell, Ibadan, Nigeria ; Mr. D. K. McE. Kevan, Nottingham ; Professor T. W. Kirkpatrick, Trinidad ; Dr. J. E. Morton, London ; Dr. T. R. E. Southwood, London ; Professor R. L. Usinger, San Francisco ; Dr. T. E. Woodward, Brisbane, Australia.

Finally, he would like to acknowledge his indebtedness to his wife for translations of German works and help in many other ways.

Reference should be made here to the excellent pioneer studies of Dufour (1833) on the internal anatomy of the Hemiptera. Considering the standard of the optical equipment of the time, the quality of this work is all the more remarkable.

II. The Female Organs.

The female reproductive organs of most Heteroptera are, except for details of the spermatheca, of somewhat uniform character. There are two laterally-placed ovaries of the acrotrophic type, each consisting of a number of ovarioles. Ovariole numbers have been investigated by Woodward (1950) and Carayon (1950*a*). As Woodward pointed out, although families may be characterised by certain prevailing numbers, there are usually exceptions. For example, in the Pentatomidae there are often seven ovarioles, but six and four have also been noted. Even within a single genus differences have been observed (Pendergrast 1950). The two lateral oviducts from the ovaries converge and form a median common oviduct which is continuous posteriorly with a passage, the

vagina, opening to the exterior. The vagina is ectodermal and possesses a cuticular lining.

When a spermatheca, or spermathecae, is present it arises from the dorsal wall of this duct. It is lined with a chitinous intima which may be thin and membranous, thick but unsclerotised or sclerotised. In some Heteroptera the organ is a simple thin-walled sac, whilst in others it shows varying degrees of complexity. It is generally possible to recognise a spermathecal duct leading from the vagina to a dilated sperm storage region, the spermathecal bulb. In some groups this bulb, or part of it, is invested by secretory cells located outside the spermathecal epithelium. In many the cuticle of the bulb can be seen to be traversed by extremely fine radial canals which are continued out as delicate tubules into the secretory cell layer. In many bugs a spermathecal pump is present. This can be a simple muscular investment of the bulb or it may be a more complex specialisation of part of the spermathecal duct. The Gerroidea possess a type of spermatheca not found elsewhere in the Heteroptera. In some groups (e.g. Miridae, Nabidae and Velocipedidae), where a spermatheca is not present, the vagina is modified to form a chamber, the bursa copulatrix, with thick cuticular walls.

Accessory glands may be present, opening into the common oviduct or into the vagina. In the latter case the gland is lined with a chitinous intima.

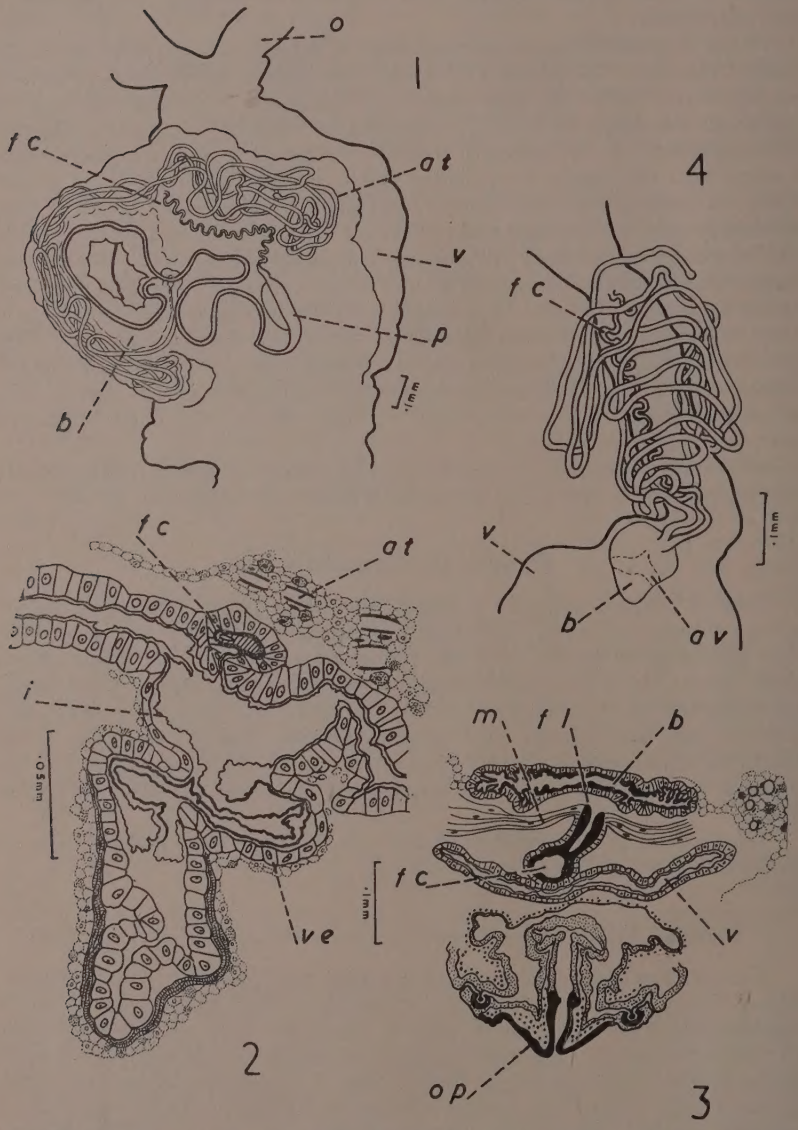
The types of spermatheca noted.

Most of the spermathecae examined have been placed into a few definite groups without difficulty. However, in some cases this has not been possible. The spermathecae of the Lygaeidae are extremely diverse and it has proved quite impossible to list spermathecal characters for the group. Some Lygaeid spermathecae are obviously close to the type found in the Berytidae and Pentatomidae, but the majority show no such affinity. The spermathecae of the Colobathristidae and Piesmidae resemble those of some Lygaeidae but the diversity is so great in this family that it would be unwise to stress relationship here.

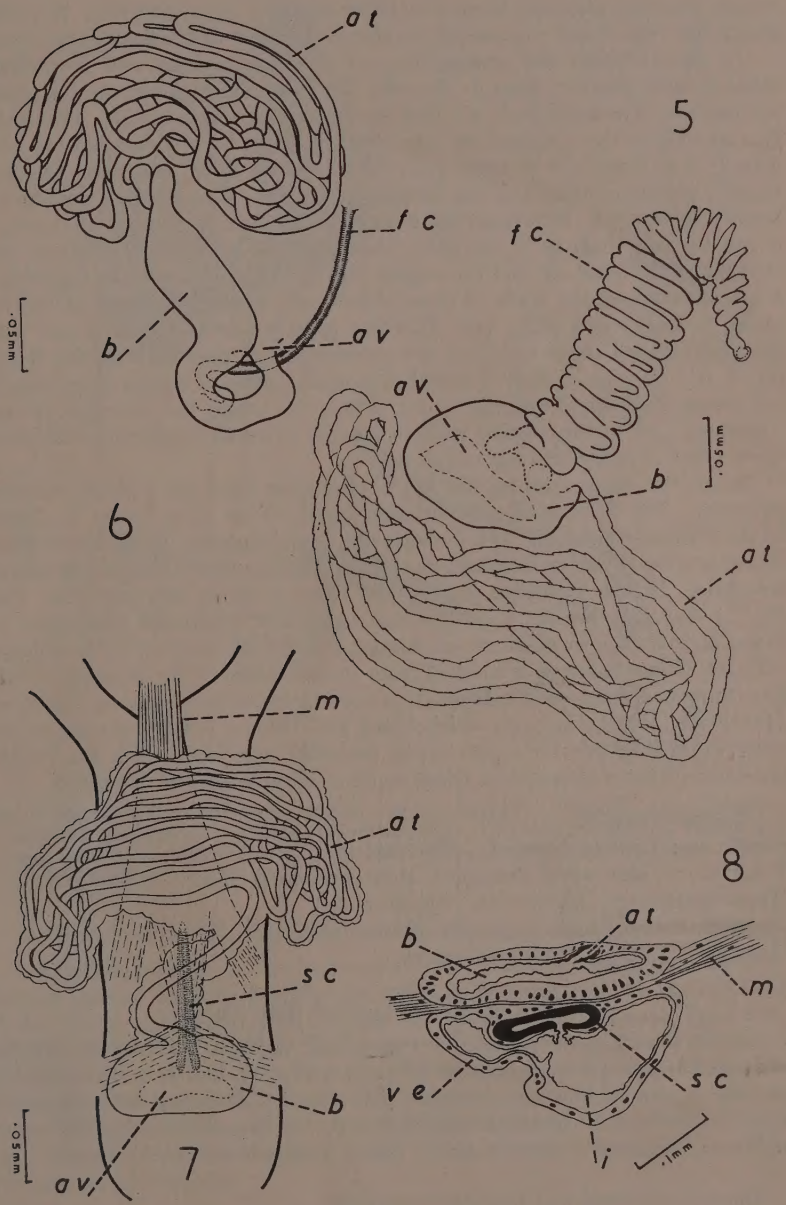
Where there is no spermatheca the type of fecundation and the form of the bursa copulatrix have been considered.

1. Gerridae, Veliidae, Hydrometridae, Mesoveliidae, Hebridae (figs. 1–9).

These groups have a spermatheca of a type not found elsewhere in the suborder. The organ consists of a basal spermathecal bulb (*b*), which is in direct communication with the vagina, and an extremely long narrow apical tube (*at*) much folded and imbedded in a mass of glandular cells and fat body. In all the species examined, except *Velia* (where it is, perhaps, present in a rudimentary form), there is a feature apparently unique in the Heteroptera—a narrow sclerotised duct (*fc*) leading forwards from the basal bulb of the spermatheca to the anterior end of the vagina. A similar structure has been noted in the Carabidae (Coleoptera) by Stein (1847) (quoted by Imms, 1948, and Heberdey, 1931). Here, it is termed the "fecundation canal", and it is believed to allow the direct passage of spermatozoa from the spermatheca to eggs in the common oviduct. The disposition of the canal in the Gerroidea points to a



FIGS. 1–4.—(1) *Gerris lacustris*, vagina and spermatheca (Gerridae). (2) *G. lacustris*, transverse section anterior region vagina, common oviduct and spermatheca. (3) *G. lacustris*, transverse section vagina, spermatheca and ovipositor at level of spermathecal pump. (4) *Hydrometra stagnorum*, vagina and spermatheca. Potash (Hydrometridae). (For key to lettering of figures see page 63.)



FIGS. 5–8.—(5) *Mesovelia furcata*, spermatheca, apical tube displaced posteriorly to expose fecundation canal. Potash (Mesoveliidae). (6) *Hebrus ruficeps*, spermatheca. Potash (Hebridae). (7) *Velia caprai*, vagina and spermatheca (Veliidae). (8) *V. caprai*, transverse section vagina and base of spermatheca.

similar function, although there is no other evidence to support this. Nevertheless, it has been found convenient to refer to this duct as the fecundation canal.

In the Gerridae the arrangement of the spermatheca and fecundation canal is more complex than in the other families, although the same elements are present. The basal bulb is a long sac lined with a thin cuticle. Proximally it is as wide as the spermatheca into which it opens by a wide aperture, while distally it narrows and is bent upon itself. At its distal end arise the long, tangled glandular tube and the fecundation canal. The latter is narrow and heavily sclerotised. By examining a series of microscope sections of the organ it can be seen that, as in the other Gerroidea, its cuticle is continuous with that lining the basal sac and the vagina (fig. 2). That is, it is to be regarded as a specialisation of the walls of these structures. About two-thirds of the way along its length is a pump (*p*). This is a greatly dilated region of the canal, the dorso-lateral parts of which are extended as a pair of wing-like flanges (fig. 3, *fl*). To each of these is attached a stout bundle of muscle fibres running out across the vaginal wall (fig. 3, *m*). From the pump the fecundation canal continues, now in the vaginal wall, in a series of small regular sinuous curves to its point of entry into the vagina.

In all the other families the apical glandular tube has a fairly constant structure. The form of the fecundation canal differs from family to family. In the Hydrometridae (fig. 4) it is short, simple and sinuous. In the Mesoveliidae (fig. 5) it is heavily sclerotised and its coils are fused to form a compact cylindrical structure. In the Hebridae (fig. 6) the canal is short and straight. *Velia* (fig. 7) does not possess a fecundation canal but sclerotised structures (*sc*) in the vaginal wall, to which muscle fibres are attached, are possibly homologous with it. This conclusion is reached from consideration of the position of these structures and from their relationships seen in transverse sections (fig. 8, *sc*). *Macrovelia* (fig. 9), however, which China and Usinger (1949) consider to be a relict which may provide a clue to the ancestral type from which the Veliidae are derived, has a fecundation canal which is close to that of *Mesovelia*.

Species examined :

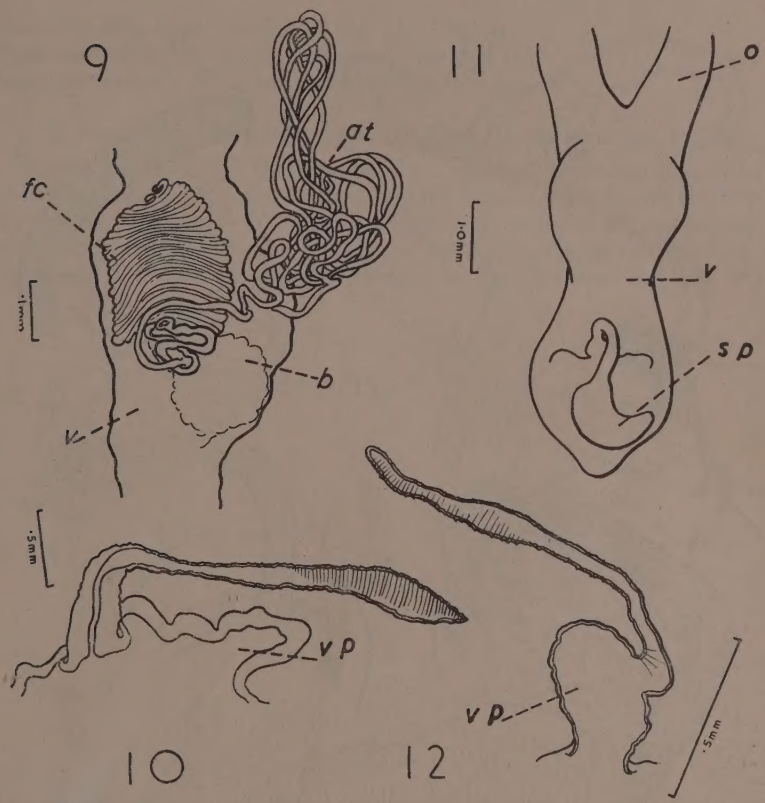
Gerridae : *Gerris lacustris* L., *Halobates* sp.
Veliidae : *Velia caprai* Tamanini, *Macrovelia horni* Uhler.
Hydrometridae : *Hydrometra stagnorum* (L.).
Mesoveliidae : *Mesovelia furcata* Mulsant and Rey.
Hebridae : *Hebrus ruficeps* (Thomson).

2. Nepidae, Belostomatidae (figs. 10–12).

Larsén (1938) has described the spermatheca of *Nepa*. In these two families the organ is a simple bent pointed tube. It is usually short but in the Belostomatidae it may be longer and narrow. It is lined with an unsclerotised cuticle which is marked with transverse striations. At the base of the organ the vaginal wall may be raised to form a pouch (the " Vaginaltasche " of Larsén).

Species examined and from the literature :

Belostomatidae : *Lethocerus niloticus* Stål (fig. 10), *Benacus griseus* Say (fig. 11), *Sphaerodema rusticum* (Fabricius) (fig. 12).
Nepidae : *Nepa cinerea* L. [Larsén, 1938].



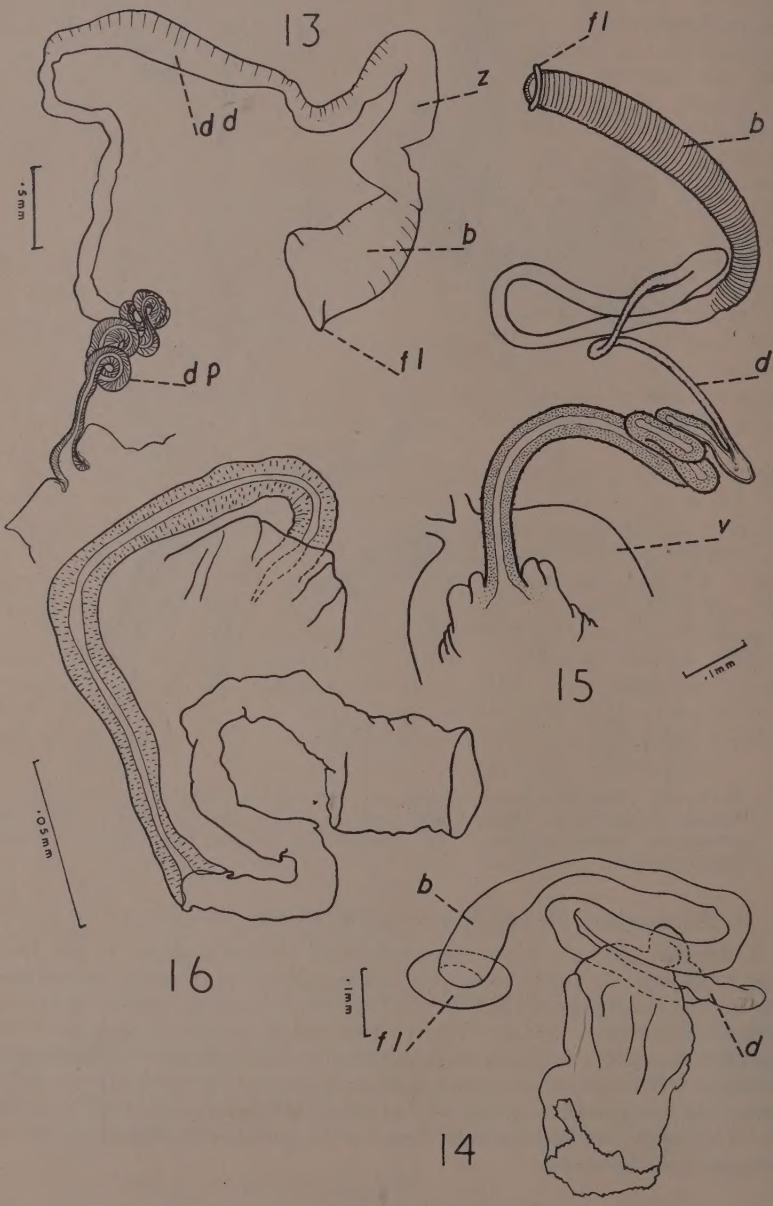
FIGS. 9–12.—(9) *Macrovelia horni*, vagina and spermatheca (Veliidae). (10) *Lethocerus niloticus*, spermatheca. Potash (Belostomatidae). (11) *Benacus griseus*, vagina and spermatheca (Belostomatidae). (12) *Sphaerodema rusticum*, spermatheca. Potash (Belostomatidae).

3. Notonectidae, Pleidae, Helotrephidae, Gelastocoridae (figs. 13–16).

A detailed account of the spermatheca of *Notonecta glauca* L. has been given by Larsén. In these families the organ is long and with an unsclerotised cuticle. The spermathecal duct is coiled and its basal parts usually lined with a characteristic thick cuticle. This part of the duct may have a glandular epithelium when the cuticle is traversed by fine canals (*Notonecta*, *Neotrephes*, *Mononyx*). The apical bulb has a thin lining and is surrounded by muscle fibres. The apical surface of the bulb is flattened, usually expanded and cap-like. This apical surface has been found to be invested by secretory cells in *Notonecta* and *Neotrephes*.

Species examined and from the literature :

NOTONECTIDAE : *Notonecta glauca* L. [Larsén], *Notonecta obliqua* Gallen (fig. 13).

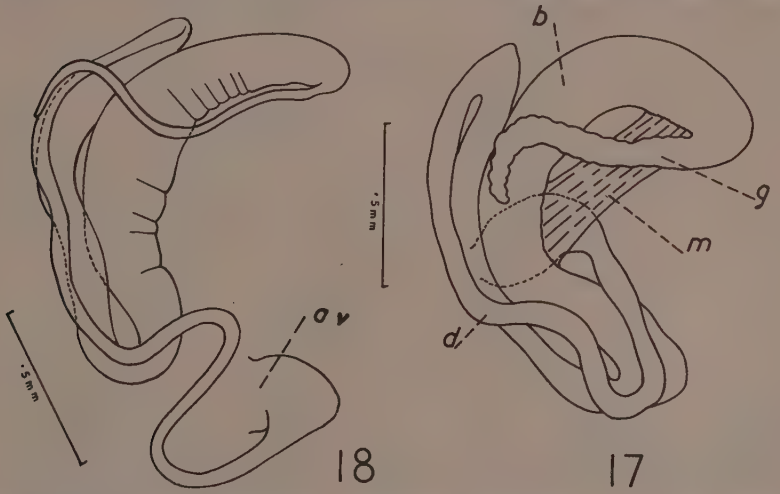


Figs. 13–16.—Spermathecae. Potash. (13) *Notonecta obliqua* (Notonectidae). (14) *Plea leachi* (Pleidae). (15) *Neotrephes usingeri* (Helotrephidae). (16) *Mononyx annulipes* (Gelastocoridae).

PLEIDAE : *Plea leachi* MacGregor (fig. 14), *Plea* sp.
HELOTREPHIDAE : *Neotrephes usingeri* China (fig. 15).
GELASTOCORIDAE : *Mononyx annulipes* Horvath (fig. 16).

4. Naucoridae, Aphelocheiridae, Corixidae, Ochteridae (figs. 17, 18).

Larsén has described the reproductive organs of *Naucoris*, *Aphelocheirus*, *Corixa* and *Sigara*. The spermatheca in these families has a narrow duct leading to a fusiform sperm bulb (*b*). The apex of the bulb is drawn out and surrounded by secretory cells (*g*). In the Naucoridae and Ochteridae it has the form of a vermiform tube bent on the sperm bulb. In the Corixidae the tube is very



FIGS. 17, 18.—*Ochterus marginatus*, spermatheca (Ochteridae): (17) Whole mount. (18) Potash.

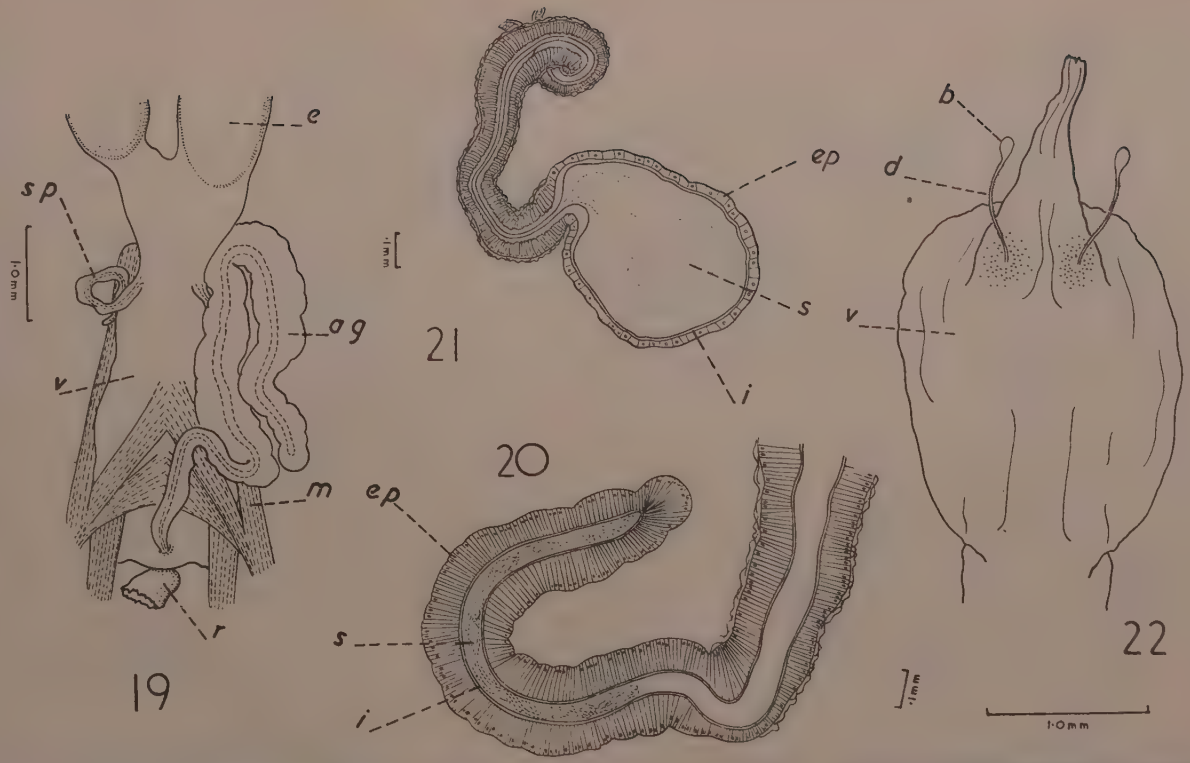
long and follows a twisted course amongst the mass of secretory cells. In *Aphelocheirus*, however, the glandular region is short, being merely the pointed apex of the sperm bulb. The sperm bulb of the Naucoridae, Aphelocheiridae and Corixidae is completely invested by muscle fibres, but in *Ochterus* the fibres form a stout muscle (*m*) stretched between the two ends of the curved sperm bulb.

Species examined and from the literature :

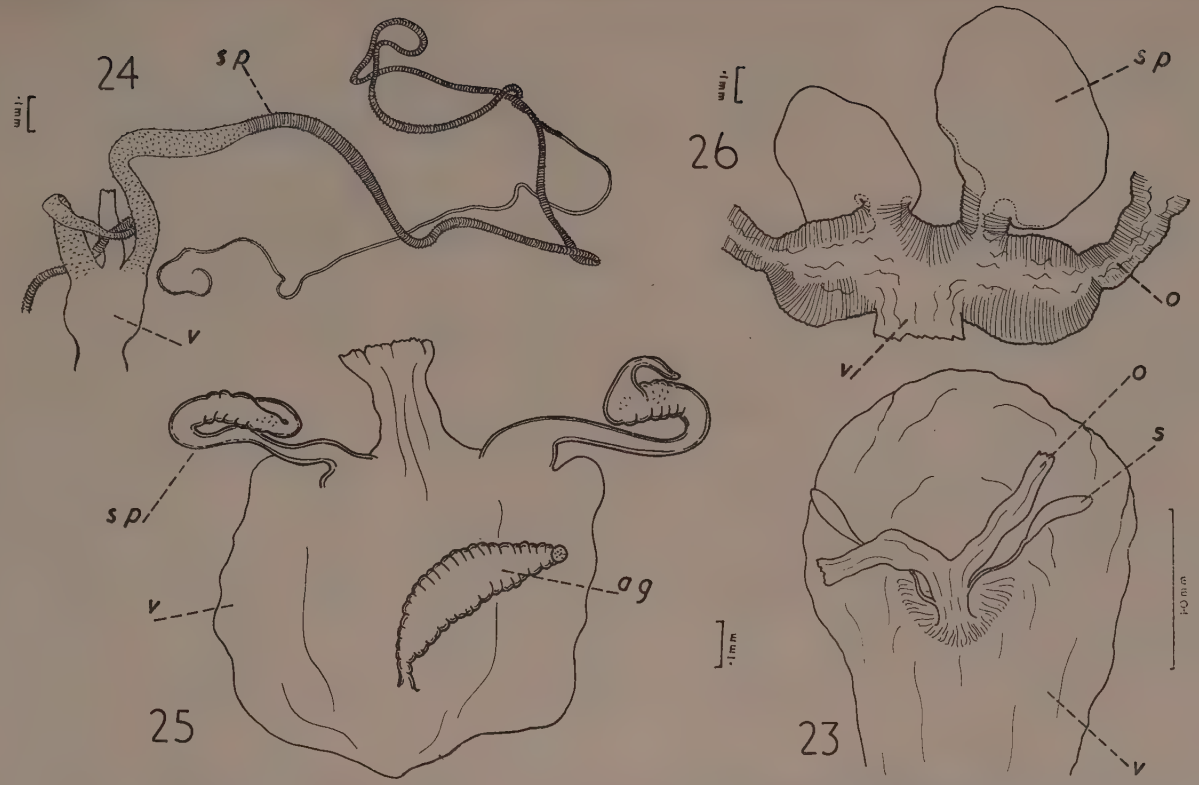
OCHTERIDAE : *Ochterus marginatus* (Latreille) (fig. 17, 18).
NAUCORIDAE : *Naucoris cimicoides* (L.) [Larsén].
APHELOCHEIRIDAE : *Aphelocheirus aestivalis* Fabricius [Larsén].
CORIXIDAE : *Corixa dentipes* (Thomson) [Larsén], *Sigara salbergi* Fieber [Larsén].

5. Reduviidae, Phymatidae, Tingidae (figs. 19–26).

All the species of Reduviidae examined, and those described by other workers, have two spermathecae. These are usually small and simple sacs



FIGS. 19–22.—(19) *Rhodnius prolixus*, female reproductive organs (Triatominae, Reduviidae). (20) *R. prolixus*, spermatheca; cleared specimen in optical section. (21) *Triatoma infestans*, spermatheca; cleared and in optical section (Triatominae, Reduviidae). (22) *Coranus subapterus*, vagina and spermathecae. Potash (Harpactocorinae, Reduviidae).



FIGS. 23-26.—(23) *Reduvius personatus*, vagina and spermatheca. Potash (Reduviinae, Reduviidae). (24) *Empicoris vagabundus*, vagina and spermatheca. Potash (Emesinae, Reduviidae). (25) *Phymata erosa*, vagina, spermatheca and accessory gland. Potash (Phymatidae). (26) *Tingis ampliata*, spermathecae. Potash (Tingidae).

or tubes opening near the anterior end of the vagina. Galliard (1935) did not observe that the spermathecae are cuticular structures in *Rhodnius* and *Triatoma* but these studies have shown that a thin unsclerotised lining is present (figs. 20, 21, *i*). The vagina is usually very large and consists of a short narrow neck-like anterior part leading into an expanded saccular posterior part. The vaginal intima is thin and unsclerotised. In *Rhodnius* and *Triatoma* the expanded vagina serves for the reception and temporary storage of spermatophores (Khalifa, 1950). Some Reduviidae have accessory glands (*ag*) opening into the posterior part of the vagina. In some there is a single gland (e.g. *Rhodnius*), in others there are two glands (e.g. *Sycanus*, described by Kershaw, 1909). The spermathecae of *Empicoris vagabundus* (Emesinae) (fig. 24) are of interest. Each is an exceedingly long, narrow, twisted tube which decreases in diameter to become thread-like distally.

The spermathecae and single accessory gland of *Phymata* (Phymatidae) (fig. 25) are similar in form to those of the Reduviidae, although the cuticle is considerably thicker.

In the Tingidae there are two saccular spermathecae arising from an expanded region at the junction of the vagina and lateral oviducts. In *Tingis* and *Stephanitis* the cuticular lining of the genital ducts is extended for some distance into the lateral oviducts.

Species examined and from the literature:

Reduviidae: *Rhodnius prolixus* Stål [Galliard and personal obs.] (figs. 19, 20), *Triatoma infestans* Klug (fig. 21), *T. rubrovaria* Blanchard [Galliard], *T. vitticeps* Stål [Galliard], *T. dimediata* (Latrielle) [Galliard], *T. protracta* Uehler [Galliard], *Coranus subapterus* (De Geer) (fig. 22), *Sycanus croceovivattus* Dohrn [Kershaw], *Reduvius personatus* (L.) (fig. 23), *Empicoris vagabundus* (L.) (fig. 24).

Phymatidae: *Phymata erosa* L. (fig. 25).

Tingidae: *Tingis ampliata* (Herrich-Schaeffer) (fig. 26), *Stephanitis rhododendri* Horvath.

6. Miridae, Anthocoridae, Microphysidae, Cimicidae, Polyctenidae, Nabidae, Velocipedidae.

There is no spermatheca. In many, very interesting methods of haemocoelic fecundation have been demonstrated by other workers. In the Miridae, Nabidae and Velocipedidae the vagina is enlarged and its intima thickened and partially sclerotised to form a structure usually termed the bursa copulatrix.

The following are the main studies on reproduction in these families: Kullenberg (1947), Miridae; Carayon (1952*d*, 1953*a*, *b*), Anthocoridae; Carayon (1949), Microphysidae; Berlese (1898), Cragg (1920), Abraham (1934), Mellanby (1939), Carayon (1952*d*), Cimicidae; Hagan (1931), Ferris and Usinger (1939), Jordan (1922), Polyctenidae; Kullenberg (1947), Carayon (1952*a*, *b*, *c*), Nabidae.

In addition the following species were examined by the writer:

Nabidae: *Nabis rugosus* (L.).

Velocipedidae: *Scotomedes alienus* Distant.

Miridae: *Leptoterna dolobrata* (L.).

7. Saldidae, Leptopodidae, Aradidae, Berytidae, Pyrrhocoridae, Coreidae, Pentatomidae, Urolabidae, Phloeidae, Cydnidae, Plataspidae (figs. 27–68).

Although there is considerable diversity in detail, the spermathecae of these families have certain common features.

There is a spermathecal duct, which may be simple or complex, leading to an apical sperm receptacle or bulb surrounded by a mass of secretory cells (fig. 42, *g*). Between the receptacle and the main part of the duct is a muscular pump consisting of a cylinder of muscle fibres surrounding the central duct. The fibres are attached at least at one end and often at both to a cuticular flange or flanges, projecting from the duct wall (fig. 42, *fd*, *fp*). When one flange is absent the fibres are attached to the duct wall or to the base of the sperm bulb.

The differences in detail often correspond to family or subfamily groupings. It is not proposed to describe them in full in this present paper. The following are the main characteristics of the spermathecae examined in these families :

Saldidae : There is a single deep pump flange, the fibres being attached distally to the bulb.

Leptopodidae : In *Leptopus* the proximal pump flange is deep and narrow (as in the Saldidae). There is a disc-like proximal flange at the base of the bulb.

Aradidae : A short cylindrical apical bulb with a distal pump flange encircling its base and with a fairly long stout pump region. The spermathecal duct is bent acutely where it leaves the pump region with the result that one side of the proximal flange is reduced.

Berytidae : The apical bulb is large, ovoid or globular, and with a thin intima. A well-developed distal pump flange encircles its base. The proximal flange is absent or poorly developed and the spermathecal duct is fairly short.

Pyrrhocoridae : There is no distal flange to the pump, the fibres being attached around the basal edge of the bulb.

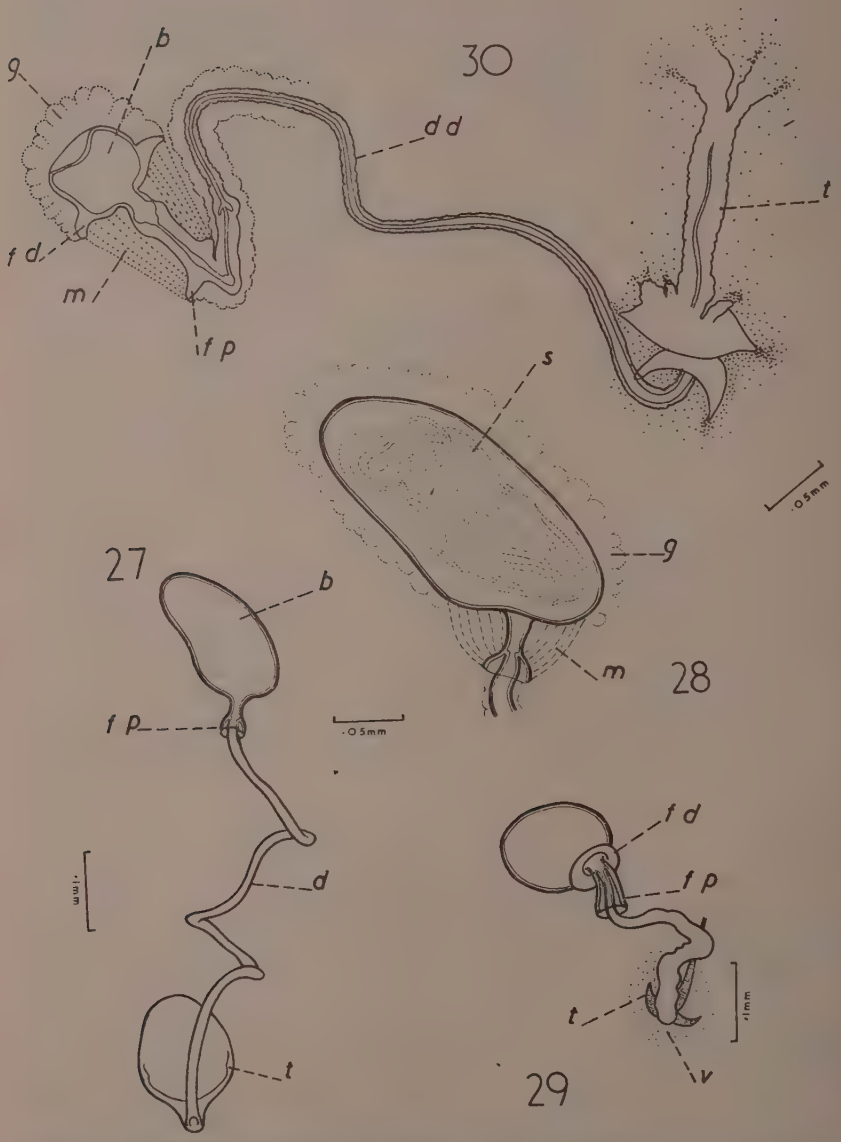
Coreidae : There is no distal flange, the muscle fibres being attached to a coiled mass of the distal parts of the spermathecal duct. Behind the pump the spermathecal duct is short or fairly short. The cuticular lining is usually thick.

Pentatomidae : There is a well-developed pumping region with two definite flanges. In this family the rest of the organ has a considerable range of form from the relatively simple type of, for example, the Acanthosominae, to the complex organ of the Pentatominae. The differences in detail will be obvious from the figures and, in addition, those considered to be of importance will be mentioned in a later section (VII) where the classification of the family is considered.

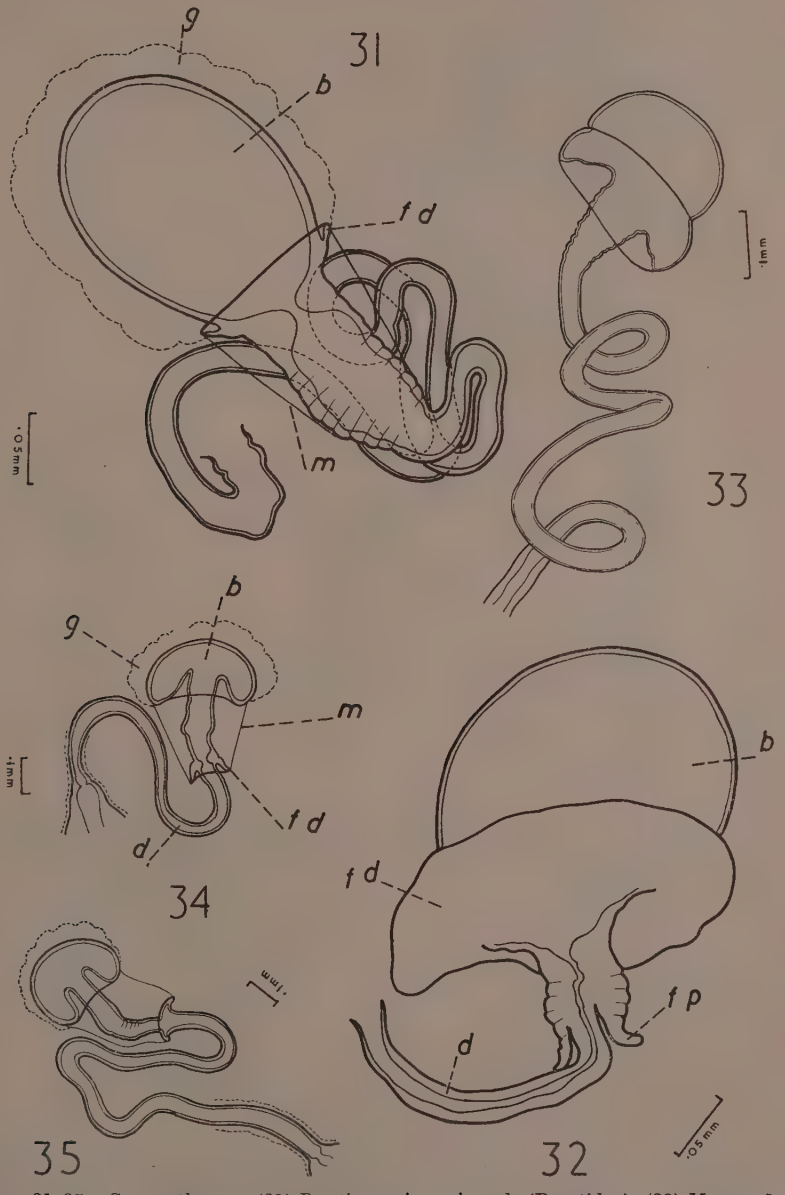
Urolabidae : In *Urolaba* the spermatheca is simple and small with a short duct. There is a single pump flange (the proximal) and the flattened sperm bulb has a blind tubular apical projection.

Phloeidae : The long pump region in *Phloeophana* has two flanges.' The middle third of the spermathecal duct has the form of a hollow ovoid dilation.

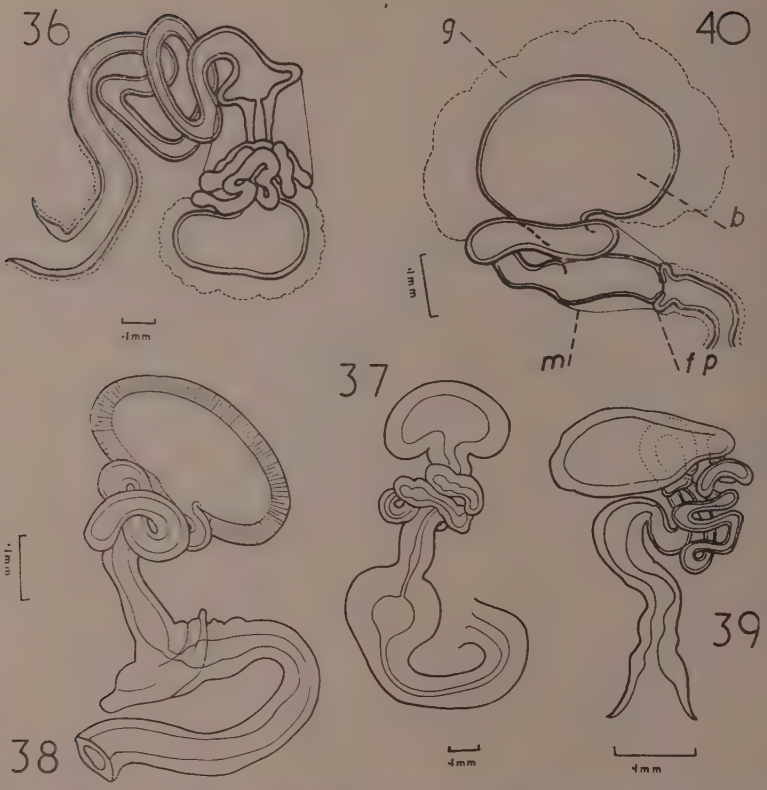
Cydnidae : The spermatheca is small. There are two flanges and the spermathecal duct has its base modified by partial invagination to form a double-walled dilation. Fusion and sclerotisation may partially obscure the structure. In one species examined (*Galgupha ovalis*) the spermathecal duct has a large thin-walled sac-like diverticulum.



FIGS. 27–30.—(27) *Saldula saltatoria*, spermatheca. Potash (Saldidae). (28) *S. saltatoria*, spermathecal bulb and pump; cleared specimen. (29) *Leptopus marmoratus*, spermatheca. Potash (Leptopodidae). (30) *Aradus cinnamomeus*, spermatheca. Potash (Aradidae).



FIGS. 31–35.—Spermathecae : (31) *Berytinus minor*, cleared. (Berytidae). (32) *Metacanthus pluto*, potash (Berytidae). (33) *Metatropis rufescens*, potash (Berytidae). (34) *Pyrrhocoris apterus*, cleared (Pyrrhocoridae). (35) *Dysdercus fasciatus*, cleared (Pyrrhocoridae).

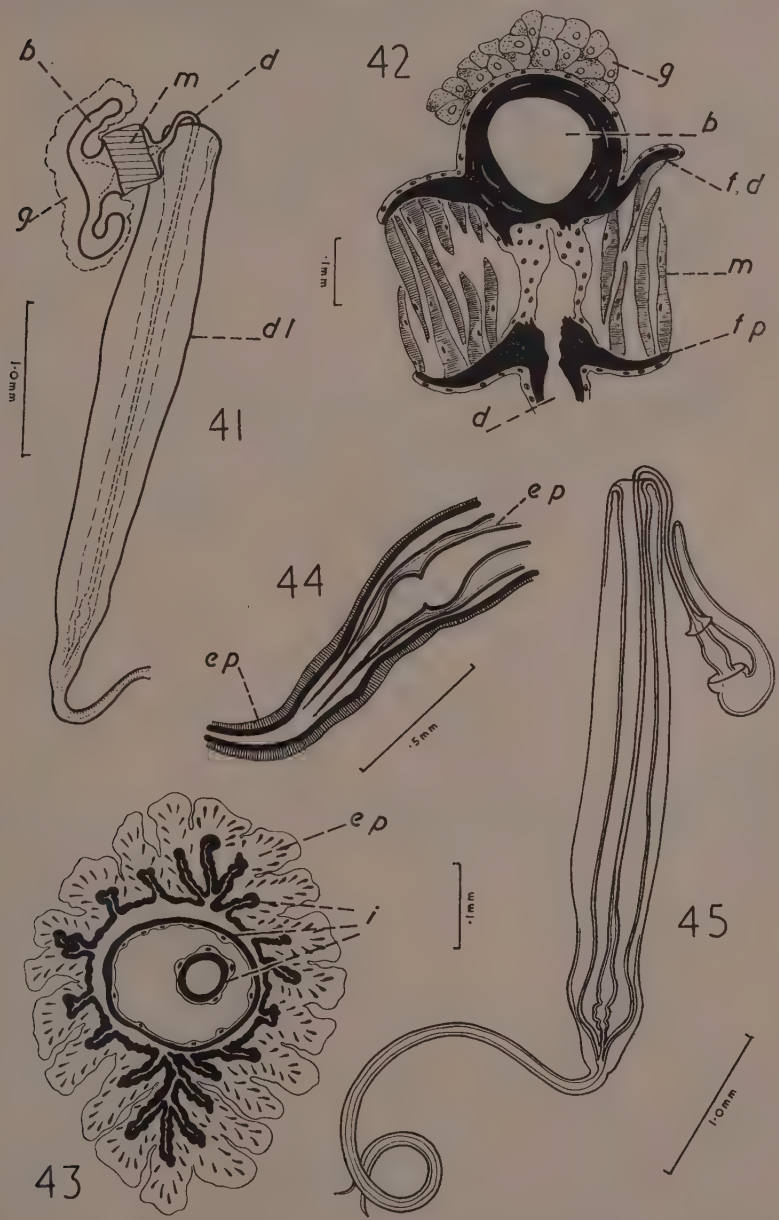


FIGS. 36–40.—Spermathecae: (36) *Coreus marginatus*, cleared (Coreinae, Coreidae). (37) *Anoplocnemis* sp., potash (Coreinae, Coreidae). (38) *Acantholybas brunneus*, potash (Coreinae, Coreidae). (39) *Coriomeris denticulatus*, potash (Pseudophloeinae, Coreidae). (40) *Myrmus miriformis*, cleared (Rhopalinae, Coreidae).

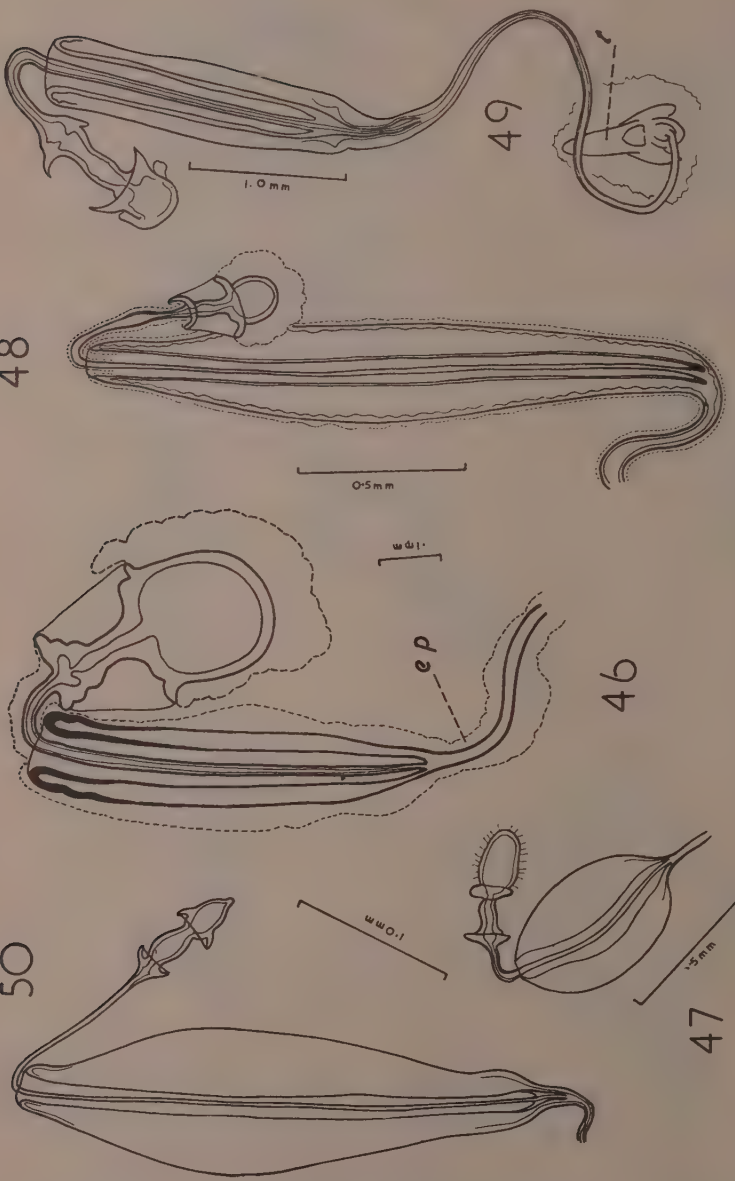
PLATASPIDAE: The spermatheca is simple. There are two stout pump flanges and the duct is short.

Species examined and from the literature:

SALDIDAE: *Saldula saltatoria* (L.) (figs. 27, 28), *S. littoralis* (L.).
LEPTOPODIDAE: *Leptopus marmoratus* Goeze (fig. 29).
ARADIDAE: *Aradus cinnamomeus* Panzer (fig. 30), *A. debilis* Uehler.
BERYTIDAE: *Berytinus minor* (Herrich-Schaeffer) (fig. 31), *Metacanthus pluto* Gross (fig. 32), *Metatropus rufescens* (Herrich-Schaeffer) (fig. 33).
PYRRHOCORIDAE: *Pyrrhocoris apterus* (L.) (fig. 34), *Dysdercus fasciatus* Signoret (fig. 35), [Freeman, 1947, figures spermathecae of 6 other species of *Dysdercus*].



FIGS. 41–45.—(41) *Nezara viridula*, spermatheca. Cleared (Pentatominae, Pentatomidae). (42) *N. viridula*, longitudinal section through spermathecal bulb and pump. (43) *N. viridula*, transverse section spermathecal duct dilation. (44) *N. viridula*, base of spermathecal duct dilation. Cleared and in optical section. (45) *Theseus modestus*, spermatheca. Potash (Pentatominae, Pentatomidae).

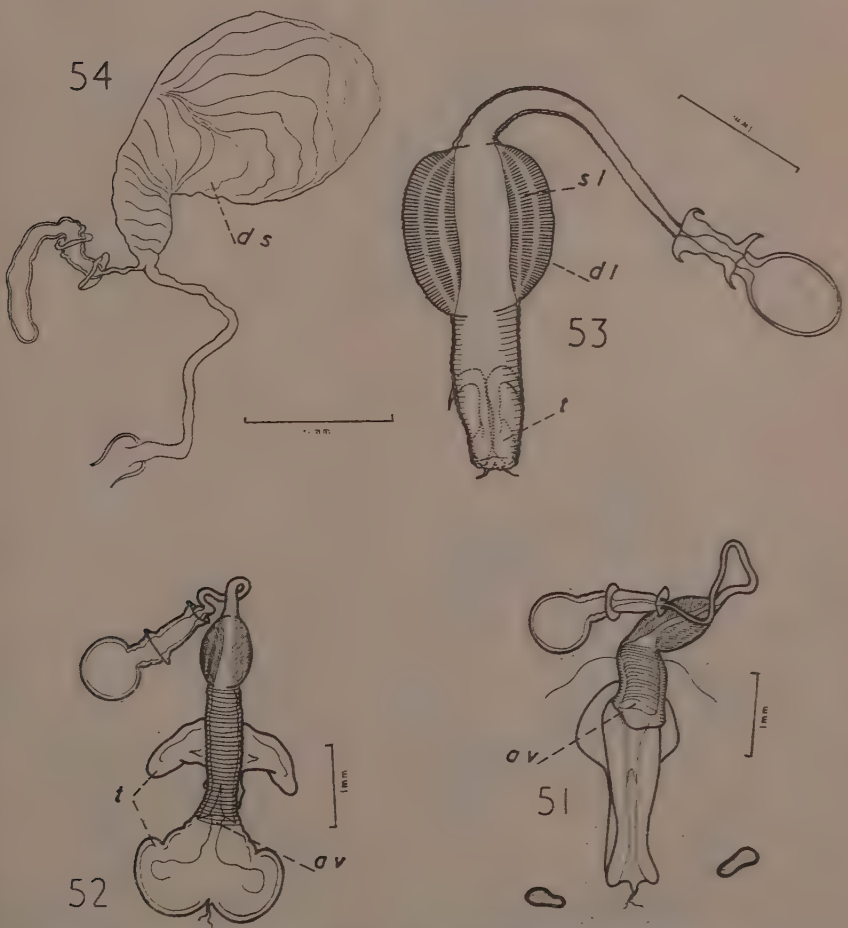


FIGS. 46–50.—Spermathecae: (46) *Cermatulus nasalis*, cleared (Asopinae, Pentatomidae). (47) *Hoplaxys coeruleus*, potash (Asopinae, Pentatomidae). (48) *Podops inuncta*, cleared (Graphosomatinae, Pentatomidae). (49) *Dalsira costalis*, potash (Phyllocephalinae, Pentatomidae). (50) *Platycarenus humilus*, potash (Discocephalinae, Pentatomidae).

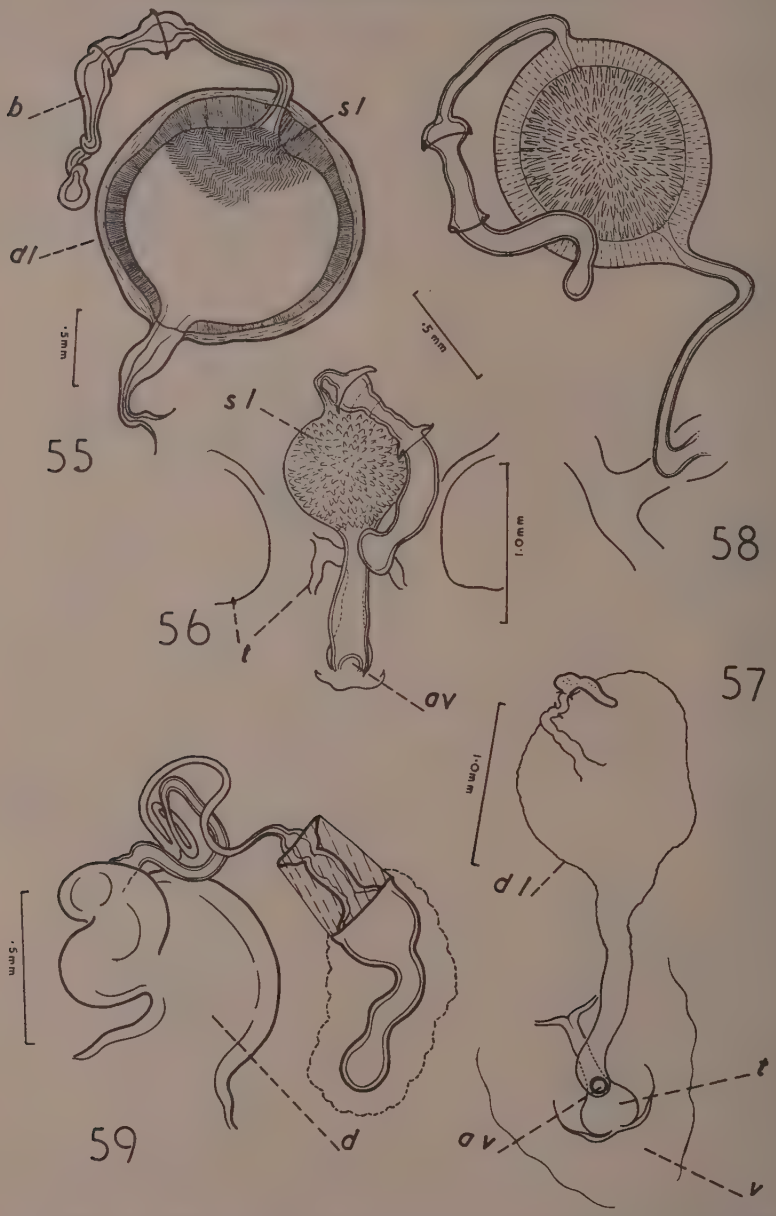
COREIDAE : *Coreus marginatus* (L.) (fig. 36), *Anoplocnemis* sp. (fig. 37), *Acantholybas brunneus* Breddin (fig. 38), *Coriomeris denticulatus* (Scopoli) (fig. 39), *Myrmus miriformis* (Fallén) (fig. 40).

PENTATOMIDAE :

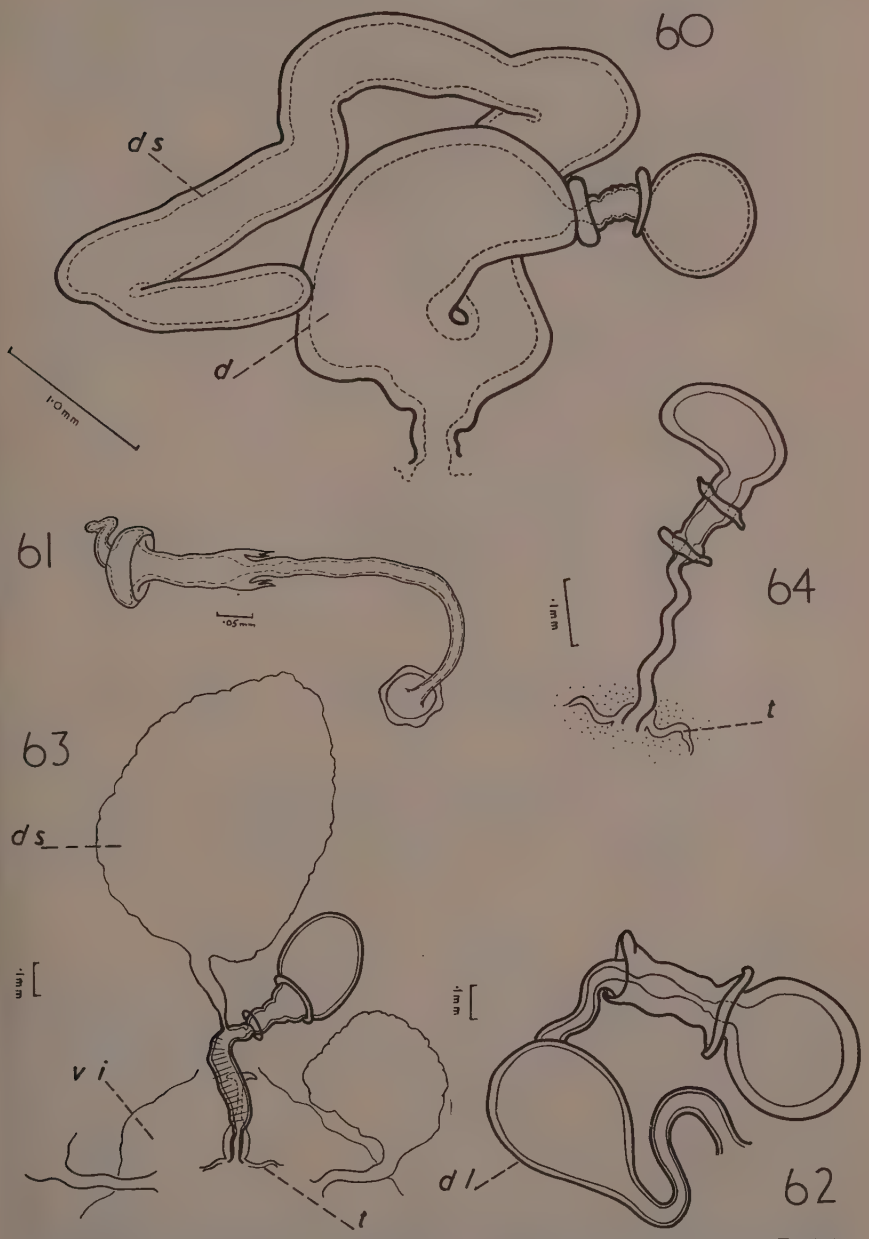
Pentatominae : *Nezara viridula* (L.) [Malouf, 1933 (inaccurate) and personal observations] (figs. 41–44), *Glaucius amyoti* (Dallas), *Dictyotus caenosus* (Westwood), *Carpocoris fuscispina* Boheman, *Eurydema ventralis* Kolenati [Bonnemaison, 1952, and personal observation], *E. ornata* (L.), *Theseus modestus* (Stål) (fig. 45).



FIGS. 51–54.—Spermathecae. Potash (All Tessaratominae, Pentatomidae). (51) *Tessaratoma javenica*. (52) *Carpona imperialis*. (53) *Phyllocoris acuta*. (54) *Rhoecocoris sulciventris*.



FIGS. 55–59.—Spermathecae. (55) *Cryptacrus comes*, potash (Scutellerinae, Pentatomidae). (56) *Scutiphora pedicellata*, potash (Scutellerinae, Pentatomidae). (57) *Tectocoris diophthalmus*, potash (Scutellerinae, Pentatomidae). (58) *Sphaerocoris annulus*, potash (Scutellerinae, Pentatomidae). (59) *Acanthosoma haemorrhoidale*, cleared (Acanthosominae, Pentatomidae).



FIGS. 60–64.—Spermathecae. Potash. (60) *Aspongopus viduatus* (Dinidorinae, Pentatomidae). (61) *Urolaba tenera* (Urolabidae). (62) *Phloeophana longirostris* (Phloeidae). (63) *Galgupha ovalis* (Cydnidae). (64) *Coptosoma inclusa* (Plataspidae).

Asopinae: *Cermatulus nasalis* (Westwood) (fig. 46), *Hoploxys coeruleus* Dallas (fig. 47), *Glypsus conspicuous* (Westwood).
Graphosomatinae: *Graphosoma italicum* Mueller [Berlese, 1899, and personal observation], *Podops inuncta* Fabricius [Leston, 1953*a*, and personal observations] (fig. 48).
Phyllocephalinae: *Dalsira costalis* (Germar) (fig. 49).
Discocephalinae: *Platycarenus humilus* (Herrich-Schaeffer) (fig. 50).
Tessaratominae: *Tessaratoma javenica* (Thunberg) (fig. 51), *Carpona imperialis* (Dohn) (fig. 52), *Phyllocoris acuta* Jeannel (fig. 53), *Rhoecocoris sulciventris* (Stål) (fig. 54).
Scutellerinae: *Cryptacrus comes* (Fabricius) (fig. 55), *Scutiphora pedicellata* (Kirby) (fig. 56), *Calidea dregii* Germar, *Tectocoris diophthalmus* (Thunberg) (fig. 57), *Sphaerocoris annulus* (Fabricius) (fig. 58).
Acanthosominae: *Acanthosoma haemorrhoidale* (L.) (fig. 59), *Rhopalimorpha lineolaris* Pendergrast, *R. obscura* White.
Dinidorinae: *Aspongopus viduatus* (Fabricius) (fig. 60).

Urolabidae: *Urolaba tenera* Westwood (fig. 61).
Phoeidae: *Phloeophana longirostris* (Spinola) (fig. 62).
Cydnidae: *Galgupha ovalis* Huss (fig. 63), *Sehirus bicolor* (L.) (fig. 65), *Macrocytus brunneus* Fabricius (fig. 66), *Thyreocoris scarabaeoides* (L.) (fig. 67).
Plastaspidae: *Coptosoma inclusa* Stål (fig. 64), *Libyaspis flavosparsa* (Montandon) (fig. 68).

8. Families in which the spermatheca shows little affinity with any of the above types.

Aëpophilidae.

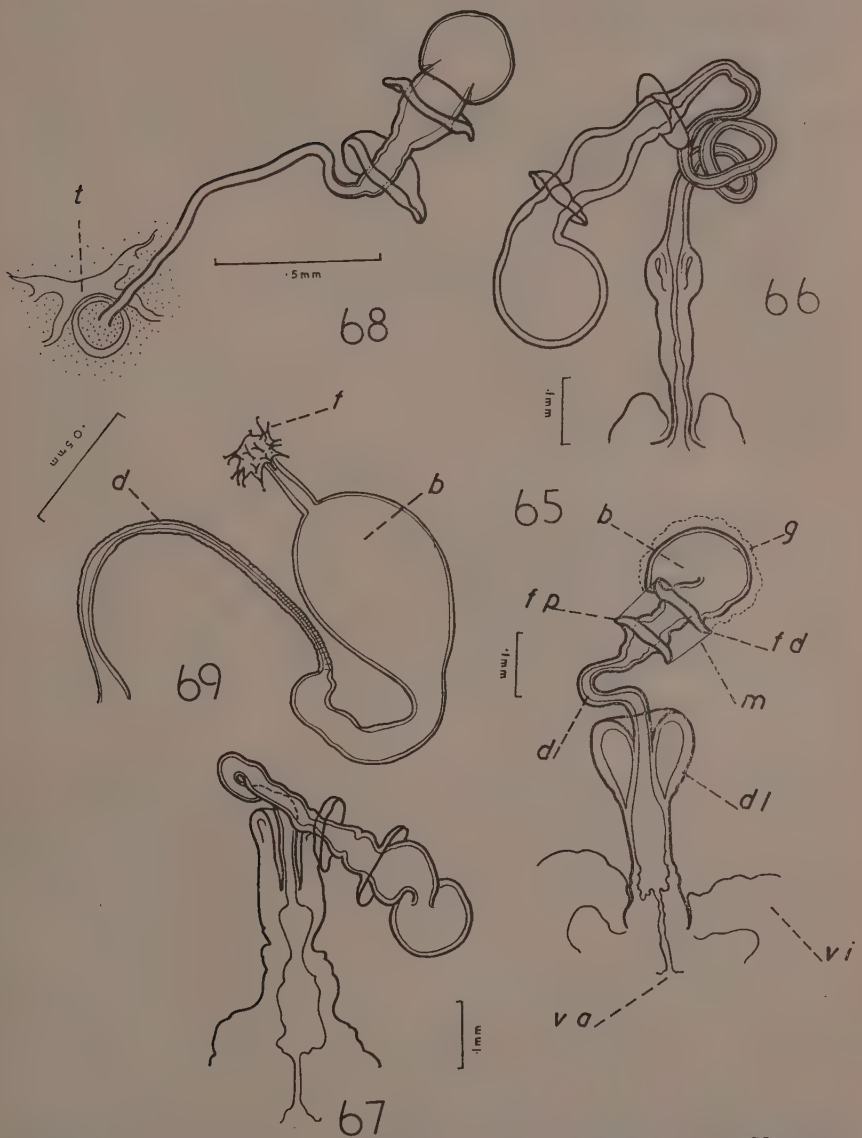
Unsatisfactory mounts of the spermatheca of *Aëpophilus bonnairei* Signoret were prepared and the author has not had further opportunity to examine females of this species. The organ seems to have a long globular apical bulb and a short wide duct. It has not been possible to determine whether there is a pumping mechanism.

Cryptostemmatidae.

The dried spermatheca of *Ceratocombus australiensis* Gross (fig. 69) has a short duct with an ovoid bulb bearing a short narrow apical canal with an expanded cap bearing a mass of ducteoles (*f*). Similar spermathecae have been figured by Wygodzinsky (1951 and 1953) for *Trichotonannus makilingensis* Wygodzinsky, *T. dundo* Wygodzinsky, *Guapinannus bierigi* Wygodzinsky and *Peloridinannus margaritatus* Wygodzinsky.

Enicocephalidae.

A single dried female of *Systelloderes maclachlani* Kirkaldy and a few specimens of *S. angustatus* (Champ.) were examined and no spermathecae were found. Carayon (1950*b*) examined fresh specimens of *Oncylocotis curculio* Karsch and reported that there is a tubular genital chamber on the dorsal wall of which is a small seminal receptacle. From the brief description it is



FIGS. 65–69.—Spermathecae. (65) *Sehirus bicolor*, cleared (Cydnidae). (66) *Macrocytus brunneus*, potash (Cydnidae). (67) *Thyreocoris scarabaeoides*, potash (Cydnidae). (68) *Libyaspis flavosparsa*, potash (Plataspidae). (69) *Ceratocombus australiensis*, potash (Cryptostemmatidae).

not clear whether the structure is a true spermatheca or a simpler specialisation of the dorsal vaginal wall.

LYGAEIDAE.

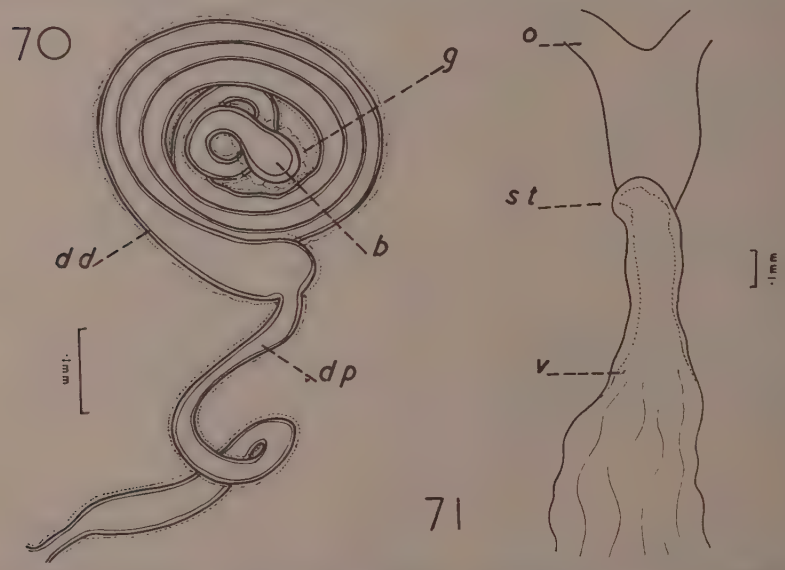
Fourteen genera from seven subfamilies were examined. A definite spermatheca was found in all these but there is a bewildering diversity in its form even amongst members of the same subfamily. It is intended to deal with this family in a separate publication.

COLOBATHRISTIDAE.

The spermatheca of *Phaenacantha sedula* Horvath is simple with a globular apical bulb and a very long irregularly-coiled duct.

PIESMIDAE.

The spermatheca of *Piesma quadratus* (Fieber) (fig. 70) has the form of a long tube with its distal parts closely coiled in a flat spiral of about four



FIGS. 70, 71.—(70) *Piesma quadratus*, spermatheca. Cleared (Piesmidae). (71) *Aneurus laevis*, vagina and common oviduct (Dysodiidae).

whorls. Its apex, which is held in the centre of the spiral, is globular and surrounded by a mass of secretory cells. Wille (1929) figured the spermatheca (" Vaginalrohr ") of this species. He did not show an apical bulb and the whorls of the duct are held in a very open coil.

DYSODIIDAE.

The spermatheca of *Mezira pacifica* Usinger is very similar to that of the Aradidae. In *Aneurus laevis* (Fabricius) (fig. 71) and *Ctenoneurus hochstetteri*

(Mayr), on the other hand, there is a simple small diverticulum of the dorsal wall of the vagina. It is surrounded by tall glandular cells. Sections of this region show sperm lying in masses of secretion in the diverticulum as well as within the anterior parts of the vagina.

9. Families for which information on the spermatheca is lacking.[1]

Leotichidae	Schizopteridae	Isometopidae
Termitaphididae	Thaumastotheriidae	Hyocephalidae
Aphylidae	Joppeicidae	

III. The Male Organs.

The male organs consist of paired testes connected by vasa deferentia with a median ductus ejaculatorius. In many groups there is a dilated region, the bulbus ejaculatorius, at the anterior end of the ductus. Accessory glands are often present. These may be of mesodermal origin (mesadenes) and open into the vasa, or ectodermal (ectadenes), in which case they are diverticula of the ductus ejaculatorius.

Except for the number of follicles or sperm tubes present, the structure of the testis is fairly uniform throughout the suborder. It consists of a number of follicles arranged more or less longitudinally and bound together by an investing peritoneal sheath. The numbers of follicles in the testes of a large number of Heteroptera have been noted by Woodward (1950), and others have been observed during this present study. These range from a single follicle in *Velia caprai* Tamanini to eight in some Miridae. Woodward has noted that in most species examined the numbers of testis follicles and ovarioles are the same. When they differ the number is usually only one greater in one sex than in the other.

The vas deferens is a simple tube with an epithelium usually invested by a muscularis of circular fibres which may become greatly thickened posteriorly. In some Heteroptera the vas is dilated apically to form a vesicula seminalis. In others it is the middle or the base which is enlarged. Where accessory glands are absent the epithelium of the vesicula may be glandular. When mesadene accessory glands are present they are usually attached to the basal half of each vas, often just prior to its entry into the bulbus ejaculatorius (e.g. fig. 100, *mg*). The gland does not pour its contents into the vas immediately, but the two canals, vas and accessory gland duct, pass back to the bulbus side by side, bound together by peritoneal membrane and often by the same muscle coat. When no bulbus ejaculatorius is present, as in the water bugs and the Gerroidea, the anterior end of the ductus ejaculatorius has a well-developed muscle coat and an epithelium of extremely tall columnar secretory cells often arranged in distinct folds (figs. 73, 78, 83). This epithelium has the same appearance as that lining the lumen of the bulbus ejaculatorius in those bugs possessing one.

[1] Since the completion of these studies, Carayon (1954) has described the sperm storage apparatus in certain families including the Isometopidae and the Joppeicidae. His observations on the families investigated by the present writer, viz. Reduviidae, Phymatidae, Tingidae and Aradidae (including Dysodiidae), in general confirm this account, although he does not regard the dorsal diverticulum in *Aneurus* as a sperm storage organ. In his studies Carayon distinguishes between a true spermatheca and other sperm storage organs.

The bulbus ejaculatorius is the complex dilated anterior end of the ductus ejaculatorius. Preliminary developmental studies indicate that the structure (with the exception of its musculature and the mesodermal vasa and mesadene ducts which enter it) is of ectodermal origin, as are the ectadenes which develop as lateral outgrowths of its dorsal wall. In its simplest form (as in the Saldidae, fig. 86) the bulbus consists of an outer saccular epithelium, termed here the investing layer (ep_1), which is continuous with that of the ductus ejaculatorius. This secretes a chitinous intima (*i*) which usually becomes separated from the cell layer and lies loosely encircling the central parts of the organ. Posteriorly it forms a tube which traverses the ductus to the aedeagus. Within the investing epithelium and its intima are two concentric epithelial layers forming a central core to the organ. The outer one, termed the middle layer (ep_2), is usually cuboidal and secretory and its cells discharge into the space within the intima. The inner layer, or lining epithelium (ep_3), is composed of very tall cells often arranged in folds. These cells are secretory and their products enter the central lumen of the bulbus which, because of the extreme tallness of the cells, is often considerably constricted. This central canal forms the duct for sperm and for mesadene secretions, the vasa and accessory gland ducts having entered it near its anterior end. As they pass back the two inner layers become reduced in diameter, fuse and eventually disappear. Thus the contents of the central canal and the products of the middle epithelium are deposited eventually within the cuticular tube of the ductus ejaculatorius through which they pass back to the aedeagus.

In some families the condition of the bulbus is not as simple as that described above. Anteriorly, the investing epithelium does not always cover the ventral side of the central core of the organ but forms, rather, a sac-like investment of its dorsal surface only, the ventral parts being invested by a thick mass of muscle fibres. This is the condition, for example, in *Dysdercus* and *Rhopalimorpha* (figs. 101, 115). In such a case the middle epithelium is also confined to the dorsal side of the lining layer and may be continuous with the investing epithelium, or almost so. When ectadenes are present they open into this dorsal sac of the bulbus. In some cases there may be large bladder-like diverticula of the dorsal sac into which the ectadenes may, or may not, open (figs. 109, *er*; 110, *es*).

The ductus ejaculatorius is a simple, thin-walled tube with an epithelium continuous with the investing layer of the bulbus (fig. 102). The cuticular lining (fig. 103*i*), which is the continuation of the loose intima of the bulbus, is usually separated from the epithelium and forms a central tube carrying the sperm and secretions of the mesadenes, the lining epithelium and the middle layer back to the aedeagus. The secretions of the ectadenes and the investing epithelium of the bulbus are, however, confined to the region outside this tube.

Although the male organs have been examined in some detail, for the purposes of classification they are probably best considered primarily on the basis of the three following characters: (*a*) the presence or absence of a definite bulbus ejaculatorius, (*b*) the presence or absence of accessory glands and, if they are present, the type of gland and (*c*) the number of follicles in the testis. Secondary characters which will be discussed are the form of the testis, the position of the vesicula seminalis, the form of the vas deferens, the presence or absence of ectodermal sacs associated with the bulbus ejaculatorius.

The types of male reproductive organs noted.

Using the three main characters it is possible to divide the types of male reproductive organs into four major groups.

1. Gerridae, Veliidae, Hydrometridae, Mesoveliidae, Hebridae (figs. 72–80).

There is no bulbus ejaculatorius, the long vas deferentia uniting to form a simple ductus ejaculatorius. The number of testis follicles is small (1 or 2). Accessory glands are absent (except in *Mesovelia*, where they are small and saccular).

In *Gerris lacustris* L. (figs. 72, 73) the reproductive organs are elongated, correlated perhaps with the lack of accessory glands. Each testis comprises two completely separate lobes, each consisting of a single follicle. Half-way along each follicle arises a short vas efferens. The vasa deferentia, vesiculae seminales and ductus ejaculatorius are all lined with a secretory epithelium.

In *Velia caprai* Tamanini (figs. 77, 78) each testis is large, ovoid and consists of a single follicle. As in *Gerris*, the ducts have a secretory epithelium. The ductus ejaculatorius is very long.

In *Hydrometra stagnorum* L. (fig. 76) the testes are long and fusiform. It is probable that each consists of a single follicle. The vesiculae seminales are long but the ductus ejaculatorius is short and narrow.

The organs in *Mesovelia furcata* Mulsant and Rey (figs. 79, 80) differ from the others in this group in being less elongated and in possessing two pairs of accessory glands which enter the dorsal aspects of the ductus ejaculatorius. Their presence causes some elaboration in the structure of the anterior parts of the ductus, which thus outwardly resembles the complex bulbus found in land bugs. However, sectioning shows this resemblance to be superficial. The testes are spherical and each comprises a single follicle. The vesiculae seminales are united at the anterior end of the ductus to form a median saccular structure.

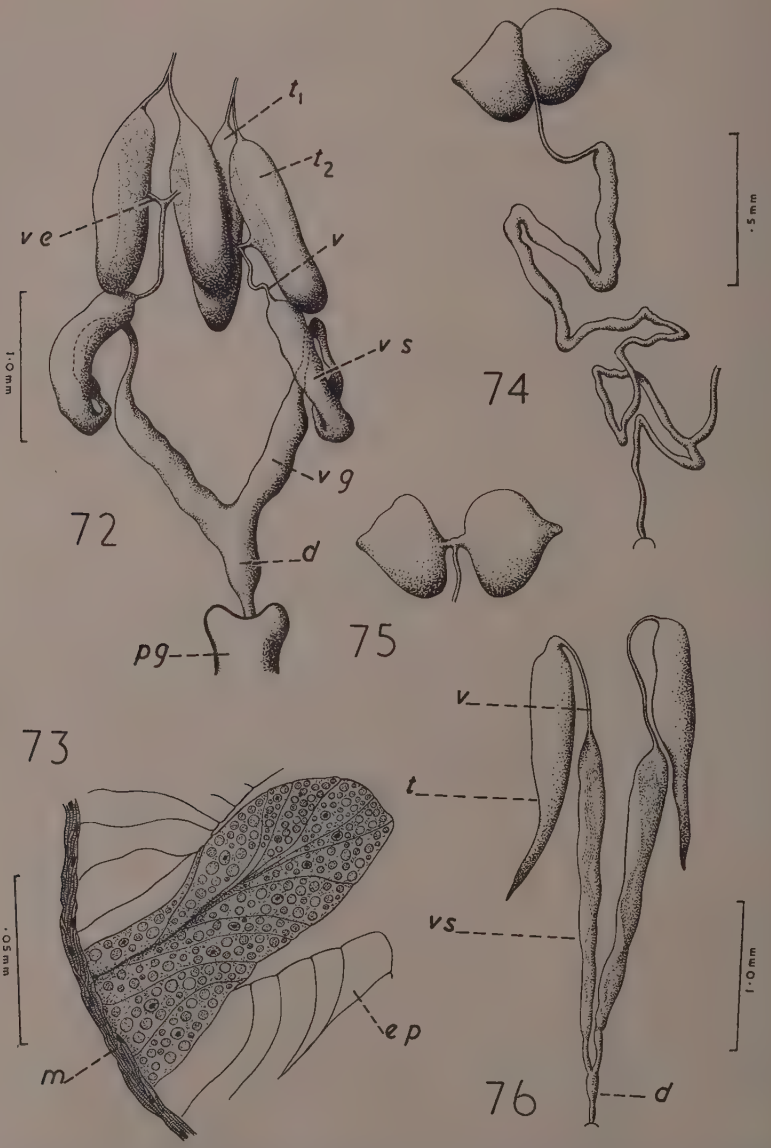
The reproductive organs of *Hebrus ruficeps* (Thomson) (figs. 74, 75) consist of a pair of bilobed testes, extremely long vasa deferentia and vesiculae seminales and a long narrow ductus ejaculatorius. Each testis consists of two conical lobes set base to base. Each lobe probably comprises a single follicle. There is a marked resemblance between the organs in *Gerris* and *Hebrus*.

2. Naucoridae, Aphelocheiridae, Belostomatidae, Nepidae, Notonectidae, Pleidae, Corixidae, Gelastocoridae, Ochteridae (figs. 81–83).

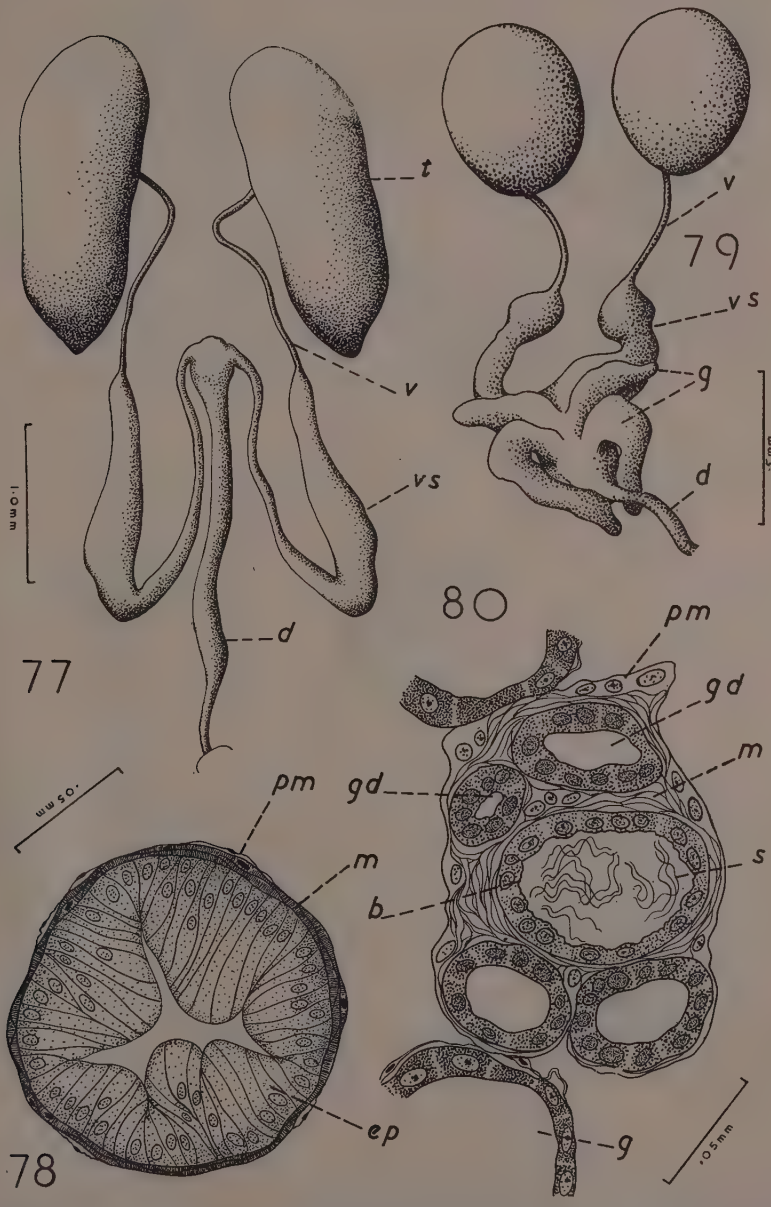
There is no bulbus ejaculatorius. Where determined, the number of testis follicles ranges between four and seven. There may be long, tubular accessory glands entering the apex of the ductus.

Larsén (1938) has given a full account of the reproductive organs in *Naucoris cimicoides* L., *Aphelocheirus aestivalis* Fabricius, *Nepa cinerea* L., *Notonecta glauca* L. and *Corixa dentipes* Thomson. Also, Rawat (1939) has described the organs in *Naucoris cimicoides*, Kerkis (1926) in *Plea atomaria* and Hamilton (1931) in *Nepa cinerea*.

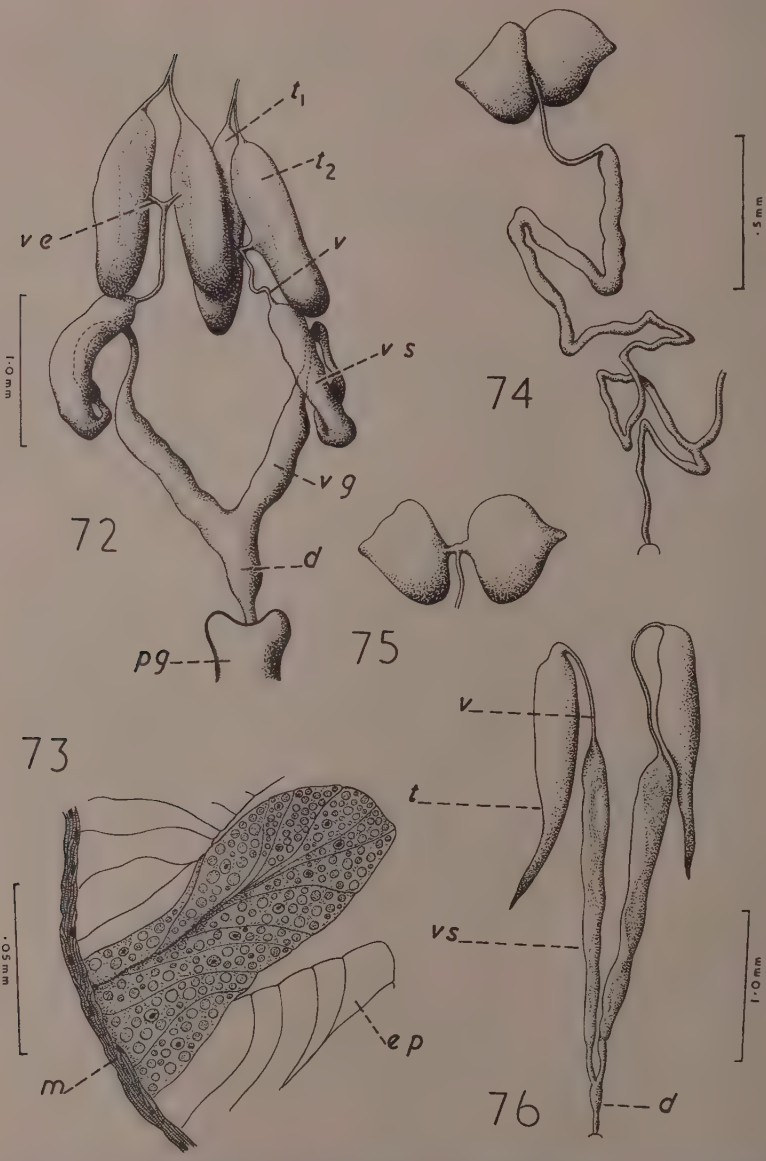
Fixed material of *Mononyx terrestris* Kevan (Gelastocoridae) was examined (fig. 81). Each testis comprises two very long lobes, the apices of which are



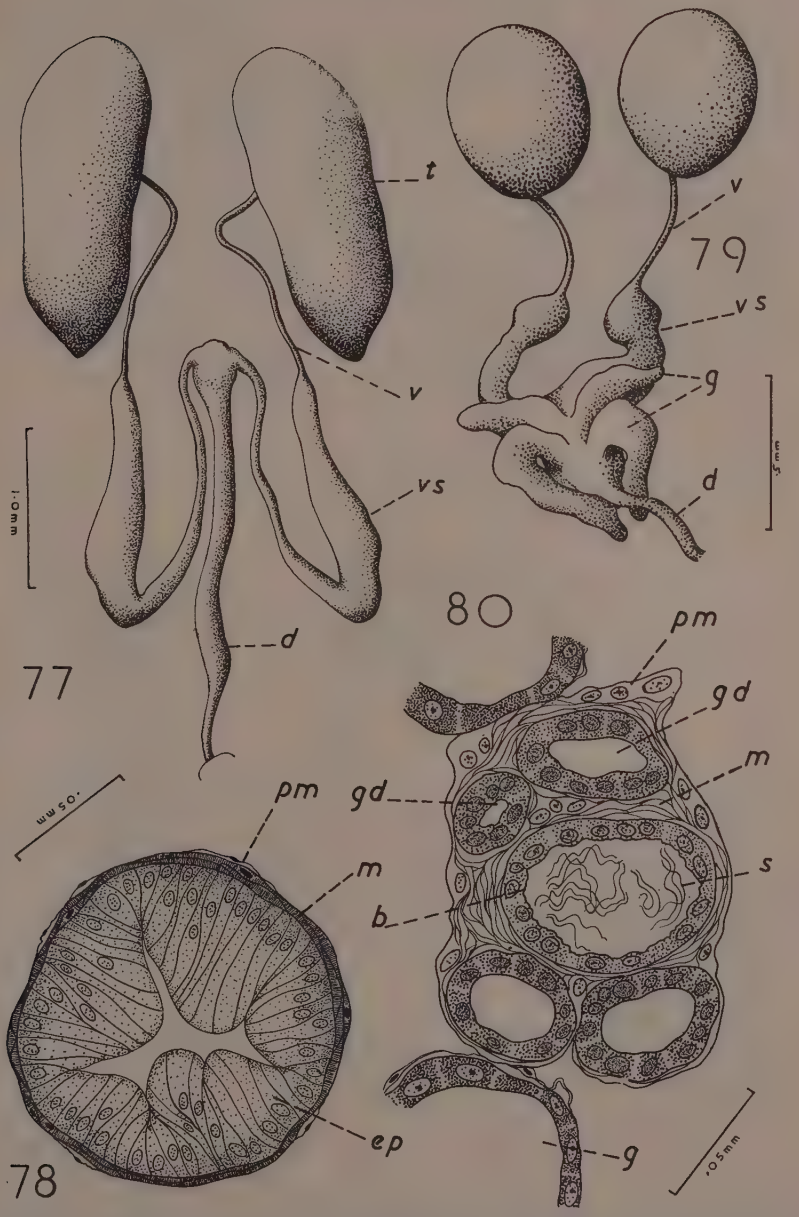
FIGS. 72–76.—(72) *Gerris lacustris*, male reproductive organs (Gerridae). (73) *G. lacustris*, transverse section to show part of wall of ductus ejaculatorius. (74) *Hebrus ruficeps*, male reproductive organs. Right testis and vas deferens omitted (Hebridae). (75) *H. ruficeps*, testis with lobes separated. (76) *Hydrometra stagnorum*, male reproductive organs (Hydrometridae).



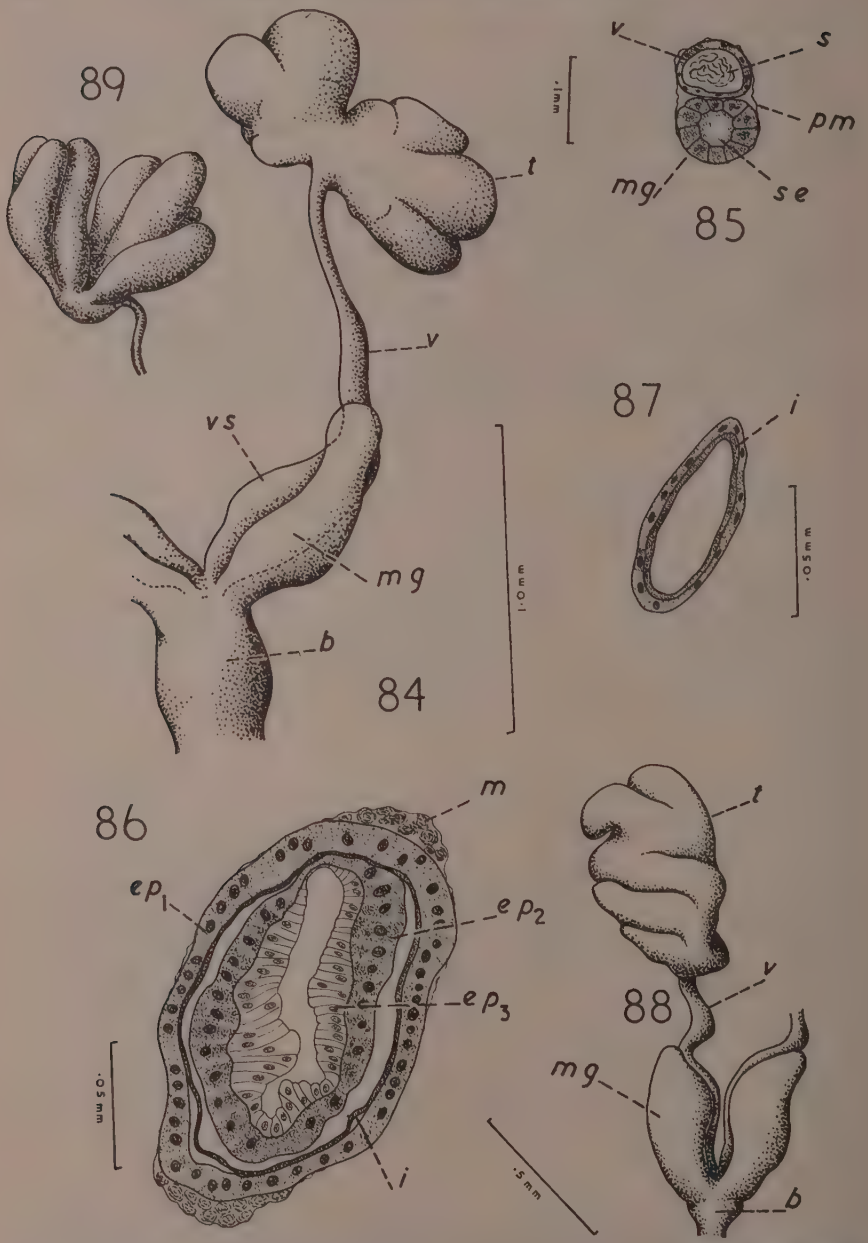
FIGS. 77–80.—(77) *Velia caprai*, male reproductive organs (Veliidae). (78) *V. caprai*, transverse section anterior end ductus ejaculatorius. (79) *Mesovelia furcata*, male reproductive organs (Mesoveliidae). (80) *M. furcata*, transverse section anterior end ductus ejaculatorius.



FIGS. 72–76.—(72) *Gerris lacustris*, male reproductive organs (Gerridae). (73) *G. lacustris*, transverse section to show part of wall of ductus ejaculatorius. (74) *Hebrus ruficeps*, male reproductive organs. Right testis and vas deferens omitted (Hebridae). (75) *H. ruficeps*, testis with lobes separated. (76) *Hydrometra stagnorum*, male reproductive organs (Hydrometridae).



FIGS. 77–80.—(77) *Velia caprai*, male reproductive organs (Veliidae). (78) *V. caprai*, transverse section anterior end ductus ejaculatorius. (79) *Mesovelia furcata*, male reproductive organs (Mesoveliidae). (80) *M. furcata*, transverse section anterior end ductus ejaculatorius.



FIGS. 84–89.—(84) *Saldula saltatoria*, male reproductive organs. Left testis and vas omitted (Saldidae). (85) *S. saltatoria*, transverse section through vas deferens and apex of accessory gland. (86) *S. saltatoria*, transverse section through bulbus. (87) *S. saltatoria*, transverse section ductus ejaculatorius. (88) *Aëpophilus bonnairei*, male reproductive organs. Right testis omitted (Aëpophilidae). (89) *A. bonnairei*, testis with follicles separated.

REDUVIIDAE.

Galliard (1935) and Carayon (1944, 1950*c*) have described male organs in some Reduviidae. In the present study those of *Sinea diadema* (Fabricius) were investigated, and this confirmed the observations of the above authors. Each testis has seven follicles. The paired mesadenes are large and each consists of four lobes meeting centrally in stellate fashion. The ductus ejaculatorius is very short. Superficially, a bulbus ejaculatorius is not apparent, but sections show that the anterior end of the ductus has a complex structure fundamentally similar to that of the typical bulbus.

PHYMATIDAE.

Carayon (1950*c*) has noted that the male organs of *Phymata* do not differ from those of typical Reduviidae.

ANTHOCORIDAE.

In *Anthocoris nemorum* (L.) (figs. 90, 91) each testis consists of four more or less spherical follicles held in line along the lateral margin of the abdomen. The distal end of the vas deferens forms the vesicula seminalis. The mesadene gland consists of several thick branched tubes which enter a spherical reservoir attached to the vas at the base of the vesicula seminalis. From here the mesadene duct passes back bound closely to the vas to enter the apex of the bulbus.

CIMICIDAE.

Christophers and Cragg (1922) and Carayon (1950*c*) have described the reproductive organs of *Cimex*. They closely resemble those of the Anthocoridae. The testes have seven follicles. It is of interest to note that Christophers and Cragg had observed that the bulbus has a complex structure, as they reported that the vasa and accessory gland ducts open at the surface of a papilla or velum projecting back into the ductus ejaculatorius.

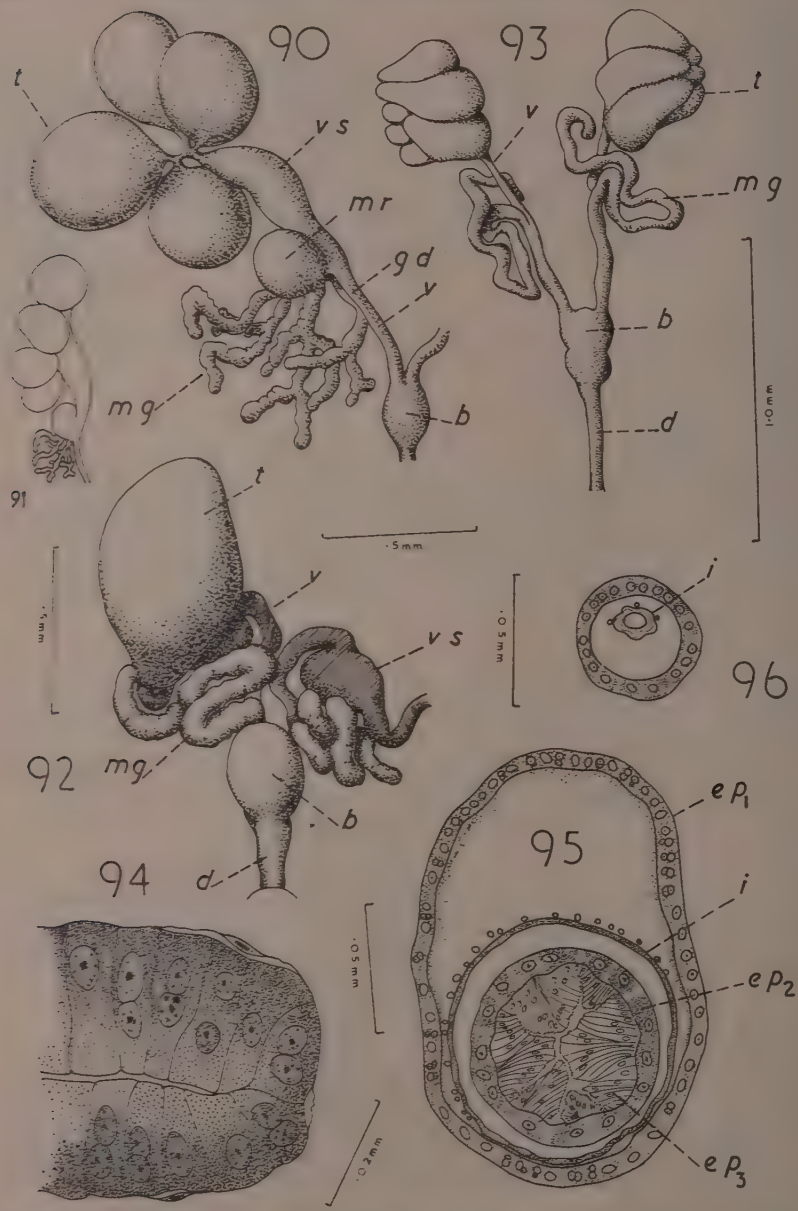
ARADIDAE.

In *Aradus cinnamomeus* Panzer (fig. 92) each testis is large and ovoid. The number of follicles has not been determined. Woodward (1950), citing Gross (1901), notes five follicles in *Aradus* sp. There are swollen vasa deferentia and a pair of tubular mesadenes. The bulbus is large.

DYSODIIDAE.

The testes of *Aneurus laevis* (Fabricius) (figs. 93–96) are somewhat pyramidal and consist of six follicles. The vas deferens is narrow and does not dilate to form a vesicula seminalis. There is a pair of mesadene glands. Each is a long coiled tube with a constricted lumen and an epithelium of very tall columnar secretory cells (fig. 94). The duct from the gland is bound to the vas by the common muscle layer.

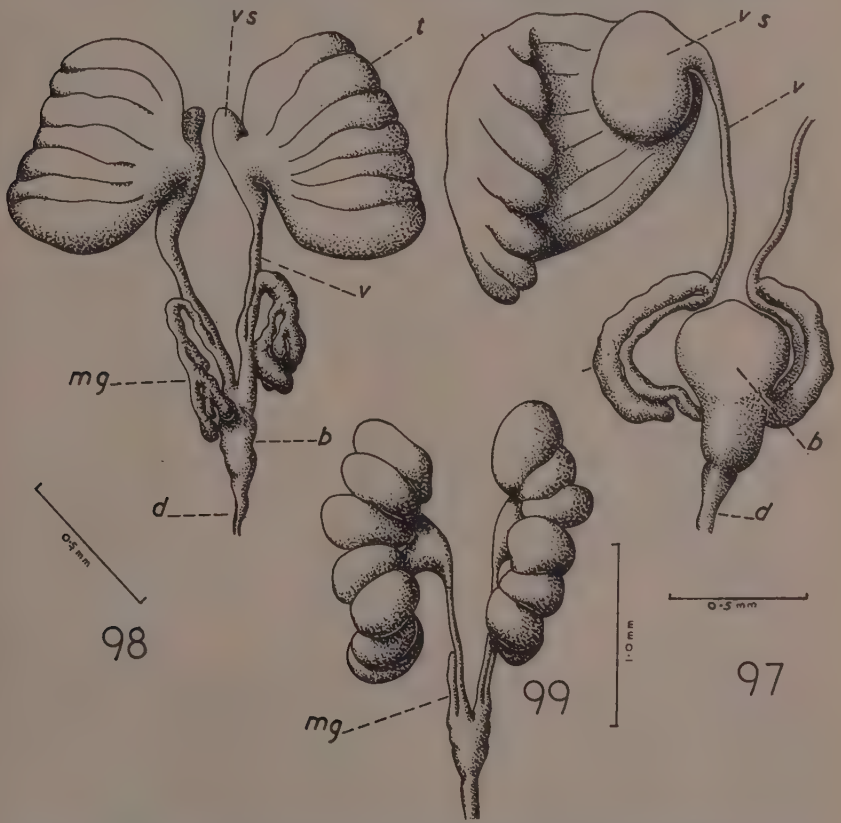
The bulbus ejaculatorius consists of the usual three cell layers. Anteriorly, the lining epithelium (ep_3) is surrounded by a thick layer of muscle fibres. This layer disappears posteriorly (fig. 95). The chitinous intima (*i*) is thick and bears numerous papillae.



FIGS. 90–96.—(90) *Anthocoris nemorum*, male reproductive organs. Testis lobes separated. Right side omitted (Anthocoridae). (91) *A. nemorum*, arrangement of testis lobes *in situ*. (92) *Aradus cinnamomeus*, male reproductive organs. Right testis omitted (Aradidae). (93) *Aneurus laevis*, male reproductive organs (Dysodiidae). (94) *A. laevis*, longitudinal section accessory gland. (95) *A. laevis*, transverse section posterior region bulbus ejaculatorius. (96) *A. laevis*, transverse section ductus ejaculatorius.

LYGAEIDAE.

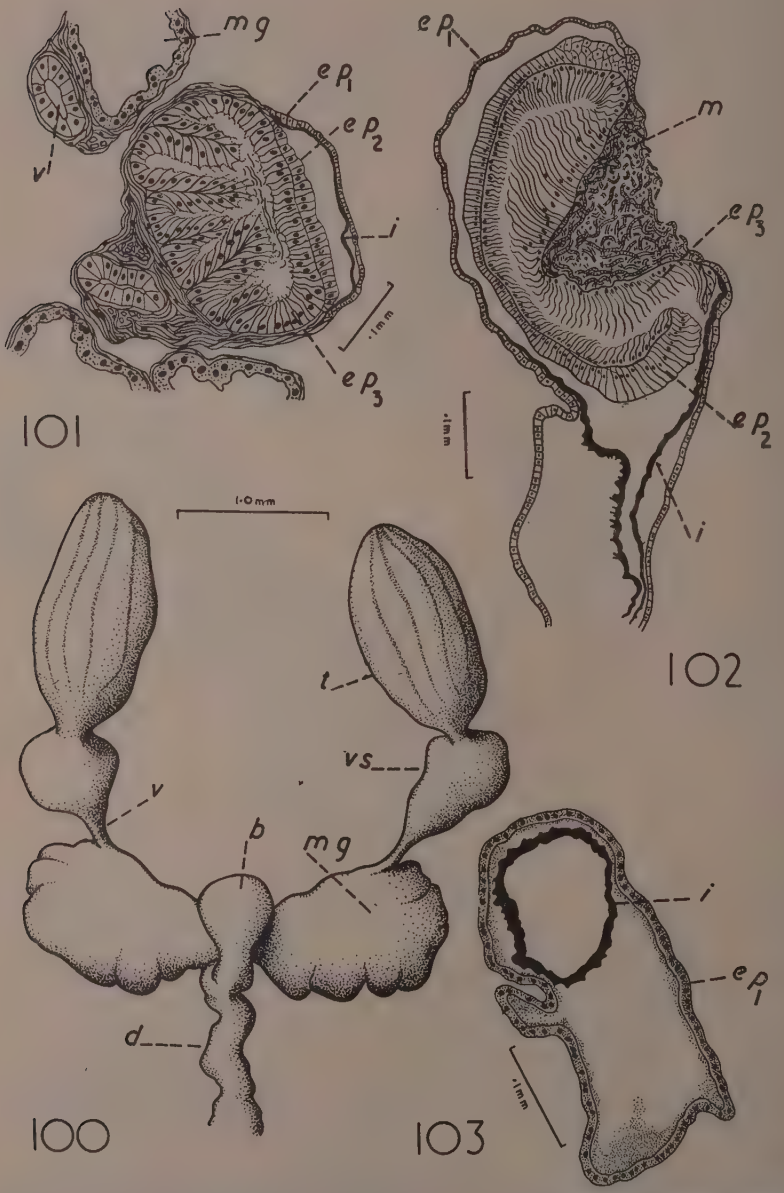
The male organs of *Kleidocerys resedae* (Panzer) (fig. 97), *Macroparius thymi* Wolff (fig. 98), *Taphropeltus contractus* (Herrich-Schaeffer) and *Ischnodemus sabuleti* (Fallén) (fig. 99) were examined. Seven follicles were noted in the testes of all these species except *Taphropeltus*, where the number was not



FIGS. 97–99.—Male reproductive organs. (97) *Kleidocerys resedae*, right testis omitted (Cyminae, Lygaeidae). (98) *Macroparius thymi* (Lygaeinae, Lygaeidae). (99) *Ischnodemus sabuleti* (Blissinae, Lygaeidae).

determined as sections were not prepared. All possess mesadenes. These are long and strap-shaped in *Kleidocerys*, lobed in *Macroparius* and reduced to small finger-like appendages in *Taphropeltus* and *Ischnodemus*. In all, the vesicula seminalis occupies the extreme anterior end of the vas deferens.

In *Kleidocerys* the vasa deferentia and associated mesadene ducts enter the large bulbus ejaculatorius very much more posteriorly than in the other Lygaeidae examined. Ludwig (1926) found a similar condition in *Lygaeus equestris* L., where the vasa enter the bulbus towards its posterior end.



FIGS. 100–103.—*Dysdercus fasciatus* (Pyrrhocoridae). (100) Male reproductive organs. (101) Transverse section bulbus ejaculatorius at point anterior to entry of vasa deferentia. (102) Longitudinal section bulbus. (103) Transverse section ductus ejaculatorius.

Bonhag and Wick (1953) have made a functional study of the reproductive organs of *Oncopeltus*. They find that the bulbus has the same complex structure as that described for the land bugs in this present study.

Berytidae.

In *Berytinus minor* (Herrich-Schaeffer) (figs. 104, 105) the testes have an unusual form. Each consists of two lobes, each comprising a single follicle. The apex of each vas deferens forms a large pear-shaped vesicula seminalis. A pair of tubular mesadene glands is present, attached to the vasa (mg_1), and unpaired short tubular glands (mg_2) enter the anterior end of the bulbus ejaculatorius. The epithelium covering the base of the bulbus is continued anteriorly on the dorsal side as a long sac (*es*) having the same structure as those found, for example, in the Pentatomidae. The anterior end of the bulbus consists of a single cell layer. Behind the base of the sac the bulbus has the usual complex structure (fig. 105), the single cell layer of the anterior region now constituting the lining epithelium (ep_3), and this is surrounded by the two more superficial layers (ep_2 and ep_1). The base of the sac can be regarded as having been folded around the lining epithelium, with its ventral wall producing the middle epithelium (ep_2) and its dorsal parts forming the outer layer (ep_1).

Pyrrhocoridae.

The testes of *Dysdercus fasciatus* Signoret (figs. 100–103) are elongate ovoid and have seven follicles each. The apical parts of the vasa form the vesiculae seminales. Each mesadene gland consists of a mass of short wide tubules bound together and to the base of the vas deferens by peritoneal membrane. The condition of the bulbus ejaculatorius (figs. 101, 102) has been referred to in the introductory section on the male organs. The organs of *Pyrrhocoris apterus* (L.) resemble those of *Dysdercus*.

Coreidae.

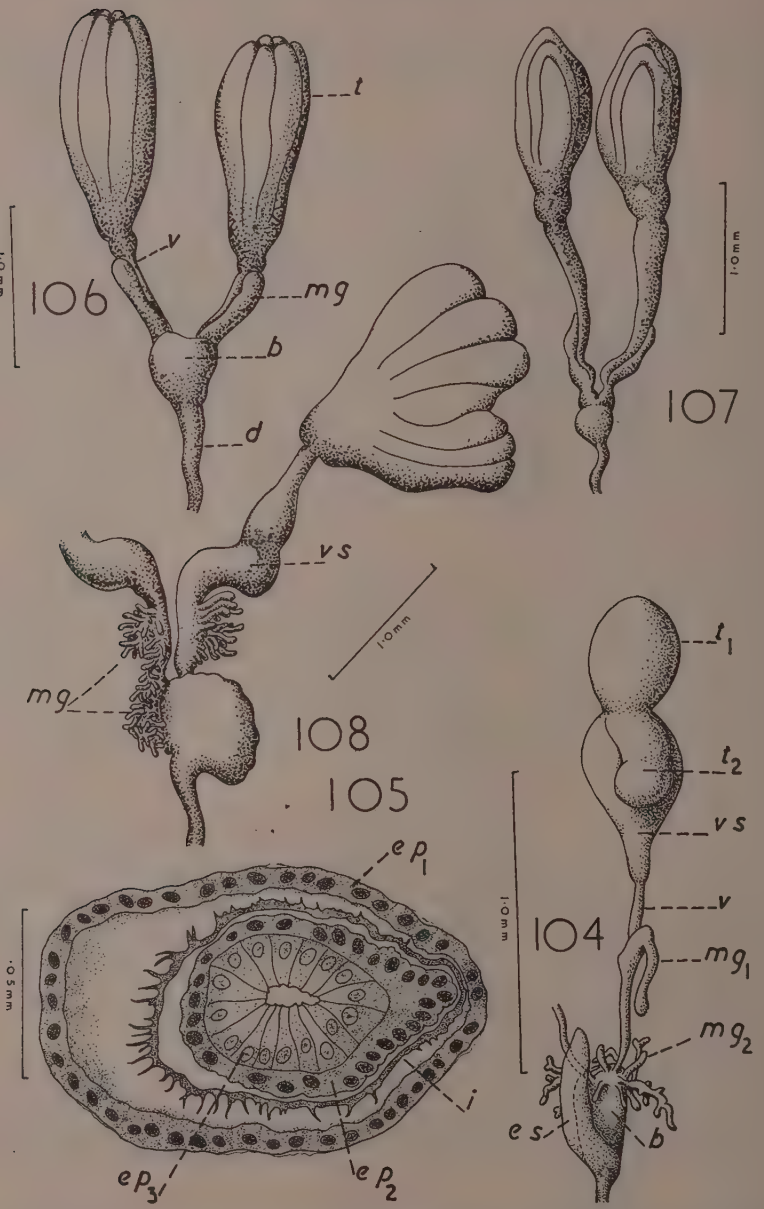
In *Rhopalus subrufus* (Gmelin) (fig. 106) and *Myrmus miriformis* (Fallén) (fig. 107) the organs resemble those of the Pyrrhocoridae, the chief difference being in the shape of the mesadene gland, which is a single wide tube closely bound to the vas by peritoneal membrane. Seven follicles are present. In *Coreus marginatus* (L.) (fig. 108) the mesadene glands consist of a large number of short tubules. The bulbus ejaculatorius is flattened and asymmetrical being displaced somewhat to one side.

Piesmidae.

The reproductive organs of *Piesma quadratus* (Fieber) (fig. 119) are very simple, consisting of large ovoid testes, simple vasa, a bulbus ejaculatorius and a short ductus. Accessory glands are absent. The number of follicles has not been determined.

Tingidae.

In *Tingis ampliata* (Herrich-Schaeffer) (fig. 120) the testes are small and more or less spherical. The number of follicles has not been determined. From each testis a fine vas deferens leads back to a long vesicula seminalis which



FIGS. 104–108.—(104) *Berytinus minor*, male reproductive organs. Left side omitted (Berytidae). (105) *B. minor*, transverse section posterior region bulbus ejaculatorius. (106) *Rhopalus subrufus*, male reproductive organs (Rhopalinae, Coreidae). (107) *Myrmus miriformis*, male reproductive organs (Rhopalinae, Coreidae). (108) *Coreus marginatus*, male reproductive organs. Left testis omitted (Coreinae, Coreidae).

enters the apex of the bulbus. Entering at this point on each side is a very long and wide mesadene accessory gland. A pair of small saccular ectadenes enter at the base of the bulbus.

Pentatomidae.

With the exception of those of the Acanthosominae, the male organs of the representatives of the subfamilies of Pentatomidae examined are characterised by a complex bulbus ejaculatorius with well-developed ectadene accessory glands in addition to the mesadenes. In many, ectodermal sacs of varying form arise from the apex or dorsal aspect of the bulbus and the ectadenes may open into these. The usual number of testis follicles seems to be six, although seven, five and four have also been found.

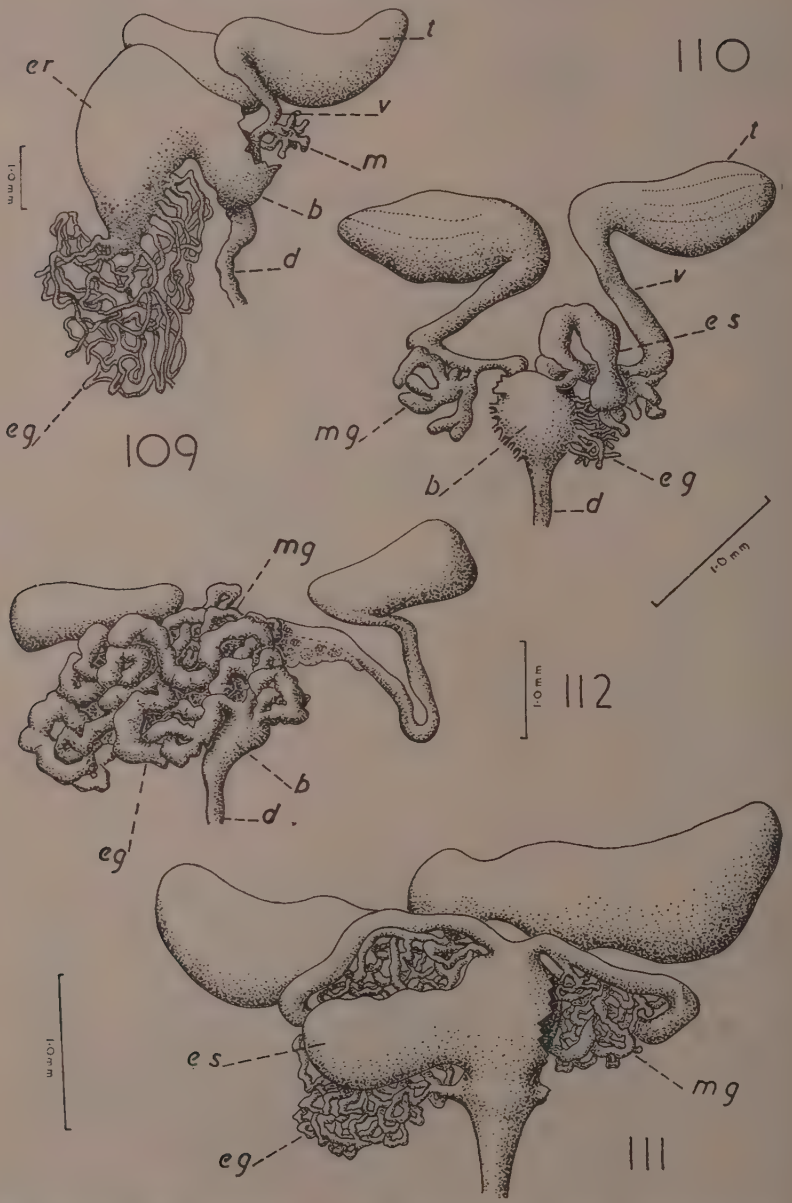
The male organs of *Nezara viridula* (L.) have already been described in detail by the writer (Pendergrast, 1956). A brief account of the condition in other species will be given here.

Pentatominae : In *Piezodorus lituratus* (Fabricius) (fig. 109) the organs resemble those of *Nezara*. The mesadene tubules are reduced in number and ectadenes open into a very large bilobed ectodermal sac. *Aëlia acuminata* (L.) (fig. 110) has the anterior ectodermal sac replaced by a pair of long strap-like sacs. The ectadene tubules open separately into the bulbus along the length of its lateral borders. *Carpocoris fuscispina* (Boheman) (fig. 111) has two separate laterally-placed ectodermal sacs. The reproductive organs of *Antestia lineaticollis* Stål, figured by Kirkpatrick (1937), resemble those of *Aëlia*. Sarel-Whitfield (1929) has given a brief description and figure of the male organs of *Agonoscelis versicolor* (Fabricius). He does not describe ectadenes, although the mass of mesadene glands in his figure extends backwards for some distance along the sides of the bulbus so there is a possibility that the ectadene tubules are included with these.

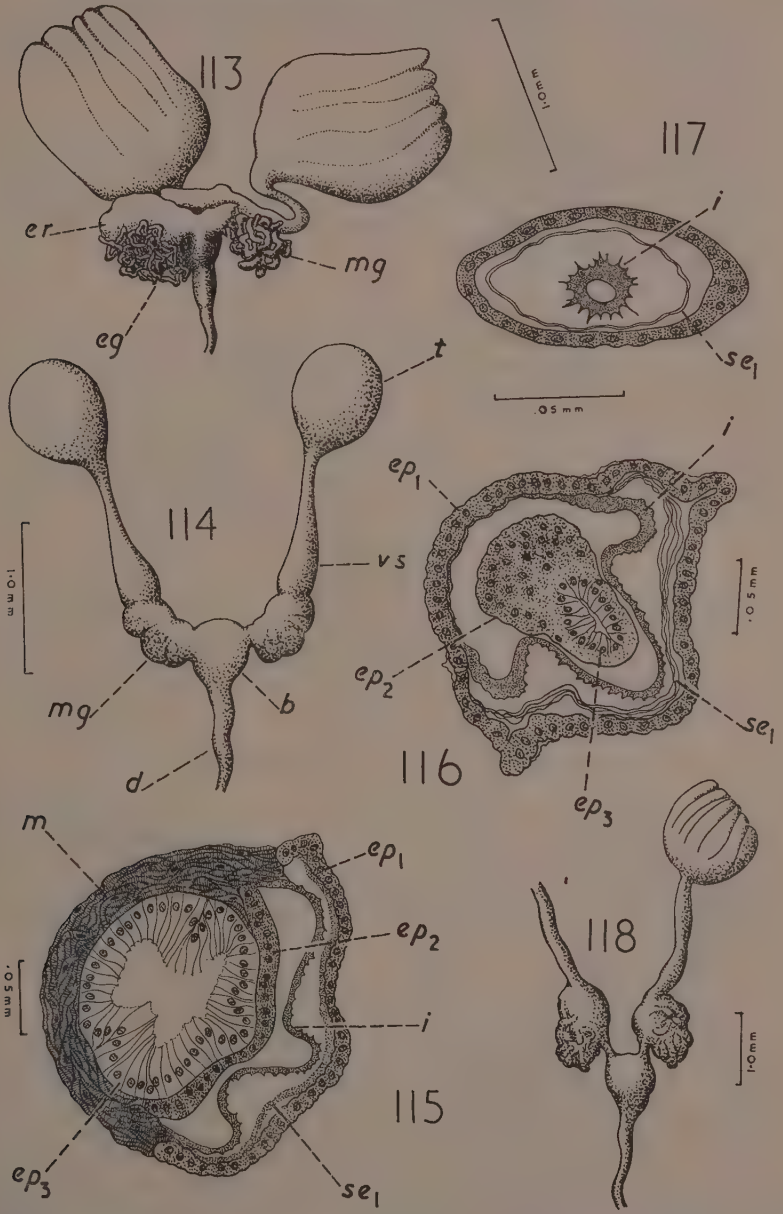
Graphosomatinae : In *Graphosoma italicum* Mueller the male reproductive organs resemble those of *Carpocoris*. Berlese (1899) has figured a diagrammatic longitudinal section of the bulbus, which shows the organ to have the same complex structure as in the Pentatominae. Seven testis follicles are present. The ectadene tubules in *Podops inuncta* (Fabricius) (fig. 113) open into the posterior edge of the ectodermal sac and not, as in *Graphosoma*, into the bulbus. There are five follicles.

Scutellerinae : In *Sphaerocoris annulus* (Fabricius) (fig. 112) both mesadene and ectadene tubules are present, the latter forming a large mass obscuring most of the bulbus, mesadenes and vasa. Ectodermal sacs are absent.

Acanthosominae : Rhopalimorpha obscura White (figs. 114–117) and *R. lineolaris* Pendergrast have similar reproductive organs, although they differ in respect of the number of testis follicles, *lineolaris* having four, and *obscura* six. The organs are somewhat simpler than those of other Pentatomidae, resembling more those of the Pyrrhocoridae. The testes are almost spherical and the mesadene glands small, consisting of a few short lobe-like tubules bound in a compact mass to the base of the vasa. The bulbus ejaculatorius is small, fusiform and lacks ectadenes and ectodermal sacs. Sections (figs. 115–117) show that it has essentially the same structure as that of *Dysdercus*. The organs of *Acanthosoma haemorrhoidale* (L.) (fig. 118) and *Elasmucha grisea*



FIGS. 109–112.—Male reproductive organs (Pentatomidae). (109) *Piezodorus lituratus*, right side of ectadene reservoir omitted to show mesadene beneath (Pentatominae). (110) *Aëlia acuminata*, left ectadene tubules omitted (Pentatominae). (111) *Carpocoris fuscispina*, right ectodermal sac and ectadene tubules omitted (Pentatominae). (112) *Sphaerocoris annulus*, some of the right mesadene tubules have been removed; their bases are seen attached to the right vas deferens (Scutellerinae).



FIGS. 113–118.—(Pentatomidae cont.). (113) *Podops inuncta*, male reproductive organs. Right ectadene and ectadene reservoir omitted (Graphosomatinae). (114) *Rhopalimorpha obscura*, male reproductive organs (Acanthosominae.) (115) *R. obscura*, transverse section bulbus ejaculatorius. (116) *R. obscura*, transverse section posterior end bulbus ejaculatorius, showing reduction in ep_2 and ep_3. (117) *R. obscura*, transverse section ductus ejaculatorius. (118) *Acanthosoma haemorrhoidale*, male reproductive organs. Left testis omitted (Acanthosominae).

(L.) resemble those of *Rhopalimorpha*. Seven testis follicles are present in both these species.

CYDNIDAE.

In *Sehirus bicolor* (L.) (fig. 121) the male organs are of the same type as those noted in the Pentatominae, the most obvious difference being the lack of tubules comprising the accessory glands, these having the form of swollen sacs. There are two pairs of ectadenes, a median ectodermal sac and a pair of mesadenes. There are seven follicles.

PLATASPIDAE.

Dissections of *Coptosoma* sp. (fig. 122) were made from alcohol material which was found to be unsuitable for dissections. The various regions were traced but details cannot be described with certainty. Each testis is large, with seven follicles. The vasa are slender, extremely long, and held in a tangled mass. The mesadenes are large glands, each consisting of a mass of wide, short tubules. The bulbus is small and receives an ectadene dorsally on each side. This is a narrow tube expanding basally to form a reservoir.

4. Miridae.

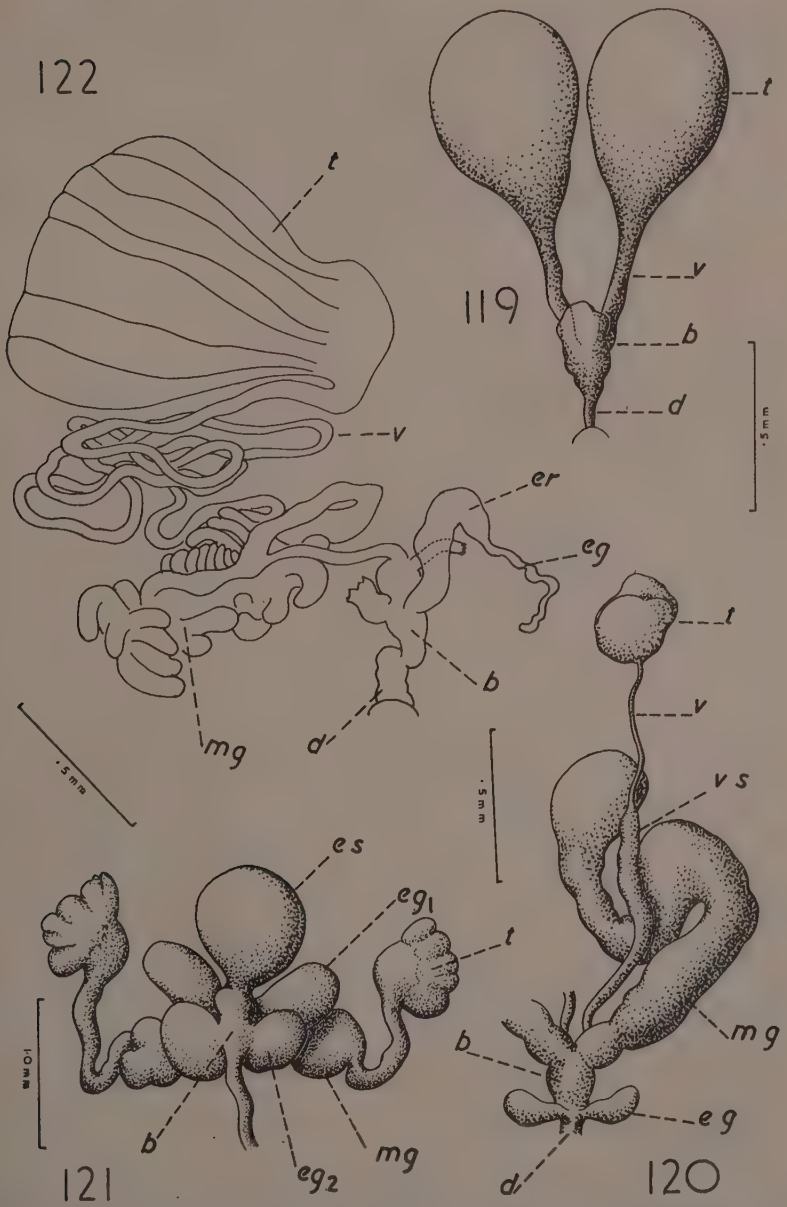
The male reproductive organs in this family are quite unlike those of other families. Kullenberg (1947) has given a very full account of the organs in a large number of species. *Calocoris ochromelas* (Gmelin), *Leptoterna dolobrata* (L.), *Notostira erratica* (L.) and *Lygus contaminatus* (Fallén) were examined by the present writer. The study confirms the account given by Kullenberg.

5. Families for which information on the male organs is lacking.

LEPTOPODIDAE.	VELOCIPEDIDAE.	CRYPTOSTEMMATIDAE.
ISOMETOPIDAE.	POECYCTENIDAE.	THAUMASTOTHERIIDAE.
COLOBATHRISTIDAE.	UROLABIDAE.	APHYLIDAE.
LEOTICHIDAE.	ENICOCEPHALIDAE.	SCHIZOPTERIDAE.
MICROPHYSIDAE.	TERMITAPHIDIDAE.	JOPPEICIDAE.
HYOCEPHALIDAE.	PHLOEIDAE.	HELOTREPHIDAE.

IV. The Reproductive Organs and Classification : Introduction.

The writer would like to stress once again that this study is primarily intended to be a morphological survey and is not an attempt to erect a system of classification on the evidence of a small group of characters. The need for caution in this respect is even more obvious when, as in this case, the data collected are relatively incomplete. Nevertheless, in this discussion it is proposed to use the evidence of the reproductive organs in an attempt to throw some light on certain aspects of Heteropteran systematics. The reasons for this are two-fold. Firstly, by so doing it is hoped that it will be possible to assess their value as characters in systematics. Secondly, it will present the evidence in a convenient form should other workers desire to incorporate it



FIGS. 119–122.—Male reproductive organs. (119) *Piesma quadratus* (Piesmidae). (120) *Tingis ampliata*, left side omitted (Tingidae). (121) *Sehirus bicolor* (Cydnidae). (122) *Coptosoma* sp., from a dissection of poorly preserved material. Arrangement of lobes of mesadene gland probably not accurate. Left ectadene gland and right mesadene, vas and testis omitted (Plataspidae).

with other evidence in future attempts to provide a classification of the suborder.

It is intended to examine the extent to which contributions to classification can be made at several different levels. These are :—

1. At the highest level in the suborder, that of the major series.
2. At the level of the superfamily and family.
3. In one group, the Pentatomidae and its related families, which has been studied rather more extensively, it is proposed to discuss the family and subfamily relationships.

V. The Major Subdivisions of the Heteroptera.

Reuter (1910) has given a review of the attempts to divide the Heteroptera into major subdivisions. The main attempts can be summarised as follows.

Latreille (1825) proposed a division into two series, the Hydrocorisae or true water bugs and the Geocorisae or land and surface-living water bugs. These divisions correspond with those of Fieber (1851) into Cryptocerata and Gymnocerata, based on antennal characters. Such a division has been followed by several authors, notably Börner (1934), Beier (1938) and Poisson (1951).

The chief points of difference in the various systems is in the placing of the Ochteridae, Gelastocoridae and Corixidae. The first two families are littoral in habit and, despite their reduced antennae, are usually placed in the Geocorisae (Gymnocerata). Beier, however, includes them in the Hydrocorisae (Cryptocerata). Börner (1904) removed the Corixidae from the Hydrocorisae to a special group, the Sandaliorrhyncha. This division was adopted by Reuter (1912). Ekblom (1929) and Spooner (1938) support this grouping, chiefly on the evidence of the mandibular levers.

Dufour (1833) proposed the addition to Latreille's Geocorisae and Hydrocorisae of a third series, the Amphibicorisae, to include the surface aquatics. This was supported by Ekblom and Spooner in their studies on the mouthparts. Thus, from the evidence they have considered, the two last-named authors would divide the Heteroptera into four series: The Sandaliorrhyncha, the Hydrocorisae, the Amphibicorisae and the Geocorisae.

Reuter (1912) arranged the families into seven major groups or series: the Sandaliorrhyncha, the Hydrobiotica, the Anonychia and four others containing only terrestrial Heteroptera. The Sandaliorrhyncha consisted of the Corixidae, while the Hydrobiotica included, in addition to the remaining water bugs, the Ochteridae, Gelastocoridae, Velocipedidae, Saldidae, Leptopodidae, Aëpophilidae, Gerridae, Veliidae and Hydrometridae. The Hebridae and Mesoveliidae were placed, along with a number of terrestrial families, in the Anonychia.

Examination of the male reproductive organs of the Heteroptera shows that, if one omits the very specialised Miridae, there is a fundamental division into two groups on the evidence of the presence or absence of the bulbus ejaculatorius. The families of the group where a bulbus is present are all included in the series Geocorisae of Poisson (1951). The other group, where the bulbus is absent, comprises the families from the Hydrocorisae, with the addition of the Gelastocoridae and Ochteridae, and the surface aquatics Gerridae, Veliidae, Hydrometridae, Mesoveliidae and Hebridae.

This division is quite clear-cut, as the bulbus ejaculatorius is not a simple dilation of the anterior end of the ductus ejaculatorius but is, in every case, a complex organ with a fundamentally uniform structure throughout the families examined. In the other group the ductus is a simple tube.

When the spermathecae are considered, a somewhat less clear-cut picture is presented. Except in the surface aquatics, the spermathecae are of interest when considered at superfamily and family level, but they do not appear to throw light on the classification at a higher grade. The spermatheca of the Gerridae, Veliidae, Hydrometridae, Mesoveliidae and Hebridae, however, differs fundamentally from all others in the Heteroptera. The presence of a second duct (the "fecundation canal"), which connects the spermathecal bulb with the anterior end of the vagina, is unique in the suborder. It is considered, therefore, that this places these families quite apart from the others in the group without a bulbus.

Concerning the Corixidae, there would seem to be a case against their removal from the Hydrocorisae to a separate series. They have male reproductive organs which are basically of the same type as those of the undisputed Hydrocorisae. This conclusion is further supported by the form of the spermatheca, which is fundamentally of the same type as that of the Naucoridae.

The evidence of the reproductive organs supports the opinion of Reuter and Beier that the Ochteridae and Gelastocoridae should be included with the Hydrocorisae. The male organs are clearly of the type found in other Hydrocorisae. The spermathecae of the two families also have clear affinities with those of the true aquatic bugs.

Considering only the reproductive organs, the writer's conclusions are :—

1. *The terrestrial bugs* (*excluding the Ochteridae and Gelastocoridae*) *form a distinct series.*—On this evidence Reuter's subdivision into several series is not justified, nor is his association of terrestrial and surface aquatic forms in both the Anonychia and the Hydrobiotica.

2. *The true aquatics* (*and the Ochteridae and Gelastocoridae*) *are a uniform and distinct group.*—The Sandaliorrhyncha would not seem a justifiable group on this evidence.

3. *The surface aquatics are a very distinct and homogeneous group.*—Reuter's separation of the Hebridae and Mesoveliidae cannot be supported, nor can the inclusion of the group in the Geocorisae be upheld. The unique character of the spermatheca in this group would seem to separate them from the true aquatic bugs.

In conclusion, considering both spermatheca and male reproductive organs, it seems that the classification most in accord with the data is a modification of Dufour's views.

(i) Male reproductive organs with a bulbus ejaculatorius . . . GEOCORISAE.
(ii) Male reproductive organs without a bulbus. Accessory glands generally present . . . . . HYDROCORISAE.
(iii) Male reproductive organs without a bulbus. Accessory glands absent (except in *Mesovelia*). Spermatheca complex, with a "fecundation canal" . . . . . AMPHIBICORISAE.

VI. Classification at the Superfamily and Family Level.

In order to arrive at some conclusions as to the points of agreement and disagreement on the classification of the Heteroptera, the systems of five authorities have been compared. These are Reuter (1912), China (1933), Börner (1943), Beier (1938) and Poisson (1951). In this section the writer proposes to indicate briefly the points of disagreement in these systems and to examine them in the light of evidence from the reproductive organs.

1. The position of the Corixidae.

In the consideration of the major series the position of the Sandaliorrhyncha has been discussed. The male reproductive organs are of the same type as those of the accepted Hydrocorisae and any differences in detail are no greater than between the other families of the series. The spermatheca of the Corixidae, although superficially different in appearance from that of *Naucoris*, is of basically the same type. Both possess a duct leading to a fusiform bulb invested by muscle fibres. Apically, this receptacle bears a glandular tube which, in the case of the Corixidae, is extremely long.

Therefore, the writer would suggest a place for the Corixidae near the Naucoridae in the series Hydrocorisae.

2. The Pleidae and Helotrephidae.

China (1933) has stated that the Notonectidae, Pleidae and Helotrephidae are three distinct families which form a natural group showing a definite sequence of specialisation amongst themselves. Poisson (1951), however, places the Pleidae and Helotrephidae in a separate superfamily, the Pleoidea, which had been proposed by Esaki and China (1928). Poisson notes that the Helotrephidae, while close to the Pleidae, also show apparent relationship with the Naucoridae.

The spermathecae of the Pleidae and Helotrephidae are clearly to be grouped with that of *Notonecta* and are unlike that of *Naucoris*. Thus the data lend support to the view of China that the Notonectidae, Pleidae and Helotrephidae should be grouped together.

3. The Ochteridae and Gelastocoridae

The position in the major series of the Ochteridae and Gelastocoridae has already been discussed. The male reproductive organs are of the same type as those of the aquatic bugs and on this evidence the writer would place them in the series Hydrocorisae.

The spermathecae of the two families differ, but each bears a close resemblance to those of certain Hydrocorisae. The spermatheca of the Ochteridae has the same form as that of the Naucoridae, possessing a long duct, curved fusiform bulb and a narrow apical glandular tube. In *Naucoris* the bulb is surrounded by a coating of muscle fibres, but in *Ochterus* these fibres form a stout band stretched between the ends of the bulb across its curvature. The spermatheca of the Gelastocoridae, on the other hand, is clearly allied to that of the Notonectidae, and appears as close to it as do those of the Pleidae and Helotrephidae.

On the evidence of the reproductive organs it would appear that: (*a*) the Ochteridae and Gelastocoridae have affinities with the Hydrocorisae and (*b*) the Telmatobia (Esaki and China, 1927) is not a natural group. This group, which has been adopted as a superfamily by Poisson (1951), includes, in addition to the Ochteridae and Gelastocoridae, the other littoral families Saldidae, Leptopodidae and Velocipedidae (Poisson omits the Velocipedidae and adds the Aëpophilidae). The three last-named families should, on reproductive characters, be included in the Geocorisae and, further, the Velocipedidae might be removed from the remaining families to a position close to the Nabidae.

4. The Notonectoidea.

Under sections 2 and 3 above, the affinity of the spermathecae of the Notonectidae, Pleidae, Helotrephidae and Gelastocoridae has been commented upon. These four families form a group within the Hydrocorisae with a uniform type of spermatheca unlike that found in the other families of the series.

Therefore, on this character, a re-definition of the Notonectoidea is suggested, to include the Gelastocoridae in addition to the Notonectidae, Pleidae and Helotrephidae. Börner's (1934) Notonectoidea, including the Naucoridae and Aphelocheiridae as well as the Notonectidae and Pleidae, is not considered to be a natural group. Nor is that of Reuter (1912) which included the Notonectidae, Naucoridae, Nepidae and Belostomatidae.

5. The Nepoidea.

Several authors (e.g. Esaki and China, 1928; Beier, 1938; Poisson, 1951) have placed the Nepidae, Belostomatidae, Naucoridae and Aphelocheiridae in the superfamily Nepoidea. The affinity of the first two families on the one hand, and the second two on the other, is also generally recognised. Esaki and China subdivide the superfamily, with the Aphelocheiridae and Naucoridae on one branch and the Belostomatidae and Nepidae on the other. Börner (1934) includes only the last two families in the Nepoidea.

The spermathecae of these two families are very similar and distinct from those of the other Hydrocorisae. There are also points of similarity in the male reproductive organs of the Nepidae and Belostomatidae.

On this basis, therefore, it would appear that the Naucoridae and Aphelocheiridae should be removed from the Nepoidea and the superfamily redefined to include only the Nepidae and Belostomatidae.

6. The Naucoridae and their allies.

The Naucoridae, Aphelocheiridae, Corixidae and Ochteridae remain after the other families of the Hydrocorisae have been placed in the redefined superfamilies noted above. Although there is a considerable diversity in the external characters of these remaining families, they can be grouped together on the evidence of the spermatheca.

It is extremely unlikely that such specialised insects as these would be brought together on the evidence of the usual taxonomic characters. Nevertheless it is convenient here to indicate their affinity with respect to the reproductive organs by their inclusion in one group.

7. The Gerroidea.

The independent status of the Gerroidea has been emphasised in Part V. It has been shown that on reproductive characters the Gerridae, Veliidae, Hydrometridae, Mesoveliidae and Hebridae should be regarded: (*a*) as a homogeneous group (in opposition to the view of Reuter, 1912); (*b*) as meriting the status of a series, the Amphibicorisae, a view which conflicts with those of many authors who place the group with either the Hydrocorisae or the Geocorisae.

Several authors have stressed the affinities of this group, or some of its families, with the Reduvioidea (e.g. Reuter, China, Beier); while Poisson notes that they have perhaps arisen from primitive Saldidae.

The unique spermatheca and the type of reproductive organs indicate that affinity with either the Reduvioidea or Saldidae is unlikely.

8. The Saldoidea.

It has been indicated in the discussion on the Ochteridae and Gelastocoridae that, on the evidence of the reproductive organs, the Telmatobia of Esaki and China (1927) is not a natural group. Reasons for the removal of the Ochteridae and Gelastocoridae have already been given. Of the remaining families, the Velocipedidae must, on reproductive characters, be placed near the Nabidae. This is discussed below in the sections on the Reduvioidea and Cimicoidea.

The remaining families are the Saldidae, Leptopodidae and Aëpophilidae. The spermathecae of the first two families are similar. It is of interest that they possess a well-developed apical pump, a character found elsewhere amongst the complex of families grouped in the Trichophora. The spermatheca of *Aëpophilus* has, unfortunately, proved difficult to examine. The male reproductive organs of *Aëpophilus* and *Saldula* have been studied and show obvious affinity.

Therefore it is concluded that the Saldidae, Leptopodidae and Aëpophilidae should remain as a group after the removal of the Ochteridae, Gelastocoridae and Velocipedidae.

9. The Reduvioidea.

It is generally agreed that there is a complex of families of predacious bugs which can be termed the Reduvioidea. However, there is considerable disagreement over the composition of the superfamily. Reuter (1912) included the Nabidae, Hebridae, Mesoveliidae, Joppeicidae, Reduviidae, Phymatidae and Enicocephalidae; while Beier adds the remainder of the Gerroidea to these. Börner, on the other hand, places in it only the Nabidae, Reduviidae and Phymatidae, and Poisson adds the Velocipedidae to these three families. China (1933) does not indicate superfamilies but in one large group he places the Phymatidae, Reduviidae and Enicocephalidae together, and somewhat apart from the Nabidae and from the five families of surface aquatics.

The Reduviidae possess paired spermathecae, a condition which has been observed elsewhere only in the Phymatidae and Tingitidae. The spermathecae and the form of the vagina and median accessory gland of the Phymatidae show clear affinity with those of the Reduviidae. Carayon (1950*c*), in discussing the male reproductive organs, notes that those of the Phymatidae are very

similar to those of the Reduviidae. In fact, he notices that both in this respect and in other characters the Emesinae (Reduviidae) differ more from the typical Reduviidae than do the Phymatidae. This opinion is borne out in these studies on the spermatheca.

The Enicocephalidae have not been examined in this study. However, Carayon (1950*b*) has noted a small median seminal receptacle. This would indicate that the family is not allied to the Reduviidae. In this connection it is of interest that Carayon (1950*b*) has remarked that the study of the eggs and other anatomical characters emphasises the great differences which separate these two families.

The Nabidae and Velocipedidae do not possess a spermatheca and, like the Miridae, they have a vagina which is modified to form a bursa copulatrix. Carayon (1950*c*) has examined the systematic position of the Nabidae and concludes that they should be placed in the Cimicoidea. He points out that the male reproductive organs of the Nabidae are unlike those of the Reduviidae but very similar to those of the Cimicidae and Anthocoridae. Blöte (1945), cited by Carayon, has demonstrated that the Velocipedidae (which he places as a subfamily of the Nabidae) share many important common characters with the Anthocoridae. The lack of spermathecae and the character of the bursa copulatrix indicate that the Nabidae and Velocipedidae should not be included in the Reduvioidea.

The Tingidae possess a large, saccular vagina and a pair of sac-like spermathecae opening into the anterior wall near the point of entry of the lateral oviducts. This character of paired spermathecae may indicate relationship with the Reduvioidea.

To sum up : The removal of the Gerroidea, the Enicocephalidae, the Nabidae and the Velocipedidae confines the superfamily Reduvioidea to the two families Reduviidae and Phymatidae, with the Tingidae as a possible addition.

10. The Cimicoidea.

There seems to be general agreement amongst the authorities that the following families constitute the superfamily Cimicoidea : Cimicidae, Anthocoridae, Miridae, Microphysidae, Polyctenidae, Isometopidae. The evidence from the reproductive organs strongly supports this grouping. (The Isometopidae have not been examined.) In these families there is no spermatheca and, in some, special mechanisms for fertilisation involving haemocoelic fecundation have been demonstrated. In the Cimicidae, Anthocoridae and Polyctenidae, Ribaga's organ, or a structure analogous to it, may be present.

Two additional families should be considered here. These are the Nabidae and Velocipedidae, both of which lack a spermatheca. These two families and the Miridae differ from the others in the development of a large bursa copulatrix by the enlargement of the vagina, and the thickening and partial sclerotisation of its cuticular lining. The bursa copulatrix of the Nabidae is very similar to that of the Miridae. The same regions are present in both, and both possess a long, median, tubular accessory gland opening into the dorsal wall of the bursa.

The male reproductive organs of the Miridae are extremely specialised and show no affinities with those of any other Heteroptera. However, those of

the Nabidae, Anthocoridae and Cimicidae have many similarities, those of the last two families being almost identical.

The conclusion reached is the same as that of Carayon (1950c and other papers), that re-definition of the Cimicoidea to include the Nabidae and Velocipedidae in addition to the undisputed families is necessary.

11. The Tingoidea.

All the authorities considered in this discussion agree that the Tingidae and Piesmidae are closely related. Evidence from the reproductive organs does not support this view. During the examination of the characters of the Reduvioidea, the form of the spermathecae of the Tingidae was discussed. In this family there are paired spermathecae opening into the anterior end of the saccular vagina. In *Piesma*, on the other hand, the spermatheca has the form of a long tube, lined with a thick cuticle and coiled apically in a regular, flat spiral.

The male reproductive organs of the Tingidae are complex, with very large mesodermal accessory glands and smaller ectodermal glands. *Piesma quadratus*, however, has extremely simple male reproductive organs, this being the only species noted amongst the Geocorisae where accessory glands are absent.

The only conclusion reached is that the Tingoidea is not a natural group, although the problem of placing the two families still remains. Possibly the Tingidae are allied to the Reduvioidea. The inclusion of the Piesmidae in Tullgren's (1918) Trichophora on the evidence of the trichobothria will be mentioned below.

12. The Trichophora.

Tullgren, in his investigation of abdominal trichobothria, termed those families where these structures occur the Heteroptera Trichophora. Those noted by him were the Pyrrhocoridae, Lygaeidae, Piesmidae, Berytidae, Coreidae, Pentatomidae and Cydnidae. Recently Leston (1953c) has reported the presence of abdominal trichobothria in the Urolabidae, Aphylidae and Phloeidae. It is apparent that the group Trichophora largely coincides with the series Polyneuria and Onychiophora of Reuter (1912).

The families in these groups have been subjected to such a variety of treatments by systematists that a brief discussion of them at superfamily level becomes extremely difficult. It has been decided not to examine the various attempts at classification at this higher level, but simply to discuss those families where evidence from the reproductive organs appears to be of interest.

China (1933) has grouped the Pentatomidae, Aphylidae, Cydnidae, Plataspidae and Phloeidae together. Near them he has placed the Urolabidae. These families are probably generally accepted to-day as consituting the Pentatomoidea (e.g. Poisson, 1951). This group will be discussed in the next section.

The spermathecae of the Lygaeidae and Colobathristidae are of little value in the examination of the higher categories. For this reason these families will not be considered here. The male reproductive organs of the Lygaeidae are of little use in attempts to establish the affinities of the group, possessing as they do features found in most Geocorisae. However, they are all characterised by the possession of a single pair of accessory glands (mesadenes) and by apically placed vesiculae seminales.

The Pyrrhocoridae have a simple spermatheca, consisting of a duct leading to an apical bulb. As in those of the Berytidae, Coreidae and Pentatomoidea there is a distinct apical muscular pump. The pump in the Pyrrhocoridae is distinctive in having a single flange (the proximal), the muscles being attached distally around the edge of the bulb. This character is also found in the Urolabidae. The similarity between the male reproductive organs and those of the Acanthosominae (Pentatomidae) is of interest, and will be noted again in a later section. The evidence from the reproductive organs is that the Pyrrhocoridae are to be allied more with the Pentatomoidea than with the Lygaeid complex of families.

All the Berytidae examined have a simple spermatheca with a large apical bulb and a poorly-developed (or absent) proximal flange of the pump. The male reproductive organs have, in addition to the pair of mesadenes, a mass of unpaired glands opening into the bulbus. There is also a large ectodermal sac attached to the bulbus. The male organs are obviously more complex than those of the Lygaeidae, Pyrrhocoridae, Coreidae and the Acanthosominae.

On the character of the spermatheca the Coreidae form a very distinct group. The spermatheca resembles those of the Pyrrhocoridae, Berytidae and Pentatomoidea in having a duct with an apical bulb and a definite pumping region. However, in all Coreidae examined, there is a proximal pump flange only, the distal ends of the muscle fibres being attached to the twisted distal parts of the spermathecal duct. Thus, the evidence from the spermatheca suggests that the Coreidae is a natural group, but does not indicate the affinities of the family.

The reproductive organs of *Piesma* show little similarity with those of any other family. Tullgren noted the presence of trichobothria and placed them in the Trichophora in the same group as the Lygaeidae. However, the diversity shown by the spermathecae of the Lygaeidae is so great that comparison is impossible. It seems that the only comment that can be made is that, as is the case with those of the Lygaeidae and Colobathristidae, the spermatheca of the Piesmidae is quite unlike those of the other families of the Trichophora.

The authorities are in general agreement that the Aradidae and Dysodiidae are close to those families which Tullgren included in the Trichophora. The evidence from the spermatheca confirms this in the case of the Aradidae, but not in that of some Dysodiidae. The Aradidae have a spermatheca with a well-developed apical pump, a character which indicates its affinity with the families of the Trichophora. Like those of the Pentatomoidea the pump has two stout flanges for the attachment of muscle fibres.

VII. Classification at Family and Subfamily Level in the Pentatomoidea.

There is general agreement amongst Heteropterists that the Pentatomoidea is a natural group. At the family level, however, the position is very different. It is probable that there is more disagreement over the family and subfamily groupings of the Pentatomoidea than in any other complex of families in the Heteroptera. Doubtless, this reflects the fact that there is possibly greater diversity here than amongst the other groups. It is hoped that evidence from the reproductive organs will contribute towards a clarification of the systematics of the superfamily.

1. The Urolabidae.

Although some authors (e.g. Reuter, 1912) have regarded this group as a subfamily of the Pentatomidae, it is usual today (e.g. China, 1933) to give it family status within the Pentatomoidea. Further evidence for a Pentatomoid relationship has recently been gained from the study of the trichobothria (Leston, 1953*b*).

There are several grounds for denying it subfamily status within the Pentatomidae. Briefly these are: the venation (Kirkaldy, 1909); the eggs (Miller, 1953); the male genitalia (Singh-Pruthi, 1925). Singh-Pruthi noted that the type of genitalia of the Urolabidae was close to that of the Acanthosominae. It will be pointed out below that there are several reasons for suggesting the removal of this latter group from the Pentatomidae. Finally, Miller (1953) has cited Yang (1939) who, in a revision of Chinese Urolabids, has suggested a relationship with the Pyrrhocoridae.

The form of the spermatheca confirms the independent status of the Urolabidae and also suggests that the group has affinities outside the Pentatomoidea. In all other Pentatomoidea the spermathecal pump has two distinct chitinous flanges. In the Urolabidae, however, there is only one, the proximal. The muscle fibres are attached distally around the basal edge of the spermathecal bulb. In this and other respects the spermatheca resembles that of the Pyrrhocoridae.

It is concluded, therefore, that although the Urolabidae are clearly Pentatomoid, there is some evidence to suggest relationships outside this superfamily and it is of interest that there should be similarities in the spermatheca and other characters with the Pyrrhocoridae. The reproductive organs of the Acanthosominae also show certain Pyrrhocorid features (see below).

2. The Plataspidae.

There is general agreement on the status of the Plataspidae. The spermatheca has the usual pentatomoid character of two distinct pump flanges. It is, however, very simple and consists of a bulb, pump region and a short, plain duct. In this respect it resembles the spermathecae of the Berytidae, Pyrrhocoridae and Urolabidae rather than those of the other Pentatomoidea. In these others the spermathecal duct is never simple.

The male reproductive organs are complex, ectadenes being present in addition to the mesadenes. The former have been noted also in the Cydnidae, Pentatomidae, Graphosomatinae and Scutellerinae. The organs of the Plataspidae are unique among those of the Trichophora in the extreme length of the vasa and the form of the accessory glands. It is interesting that in the Plataspidae, where the externals and the male reproductive organs are very specialised, the spermatheca has remained in the simple condition.

Thus, the evidence of the male and female reproductive organs confirms the placing of this group as a separate family within the Pentatomoidea.

3. The Phloeidae.

The position and status of this group has been the subject of an investigation by Leston (1953*c*). This author demonstrates that the group is correctly placed

in the Pentatomoidea and gives reasons for regarding it as a separate family. Thus, his findings are in accord with those of China (1933) and Poisson (1951).

The spermatheca of the Phloeidae is pentatomoid in having two pump flanges but is distinct from those of the other families and subfamilies. The spermathecal duct has a simple, ovoid dilation unlike that of the other groups. This evidence, therefore, tends to confirm the family status of the Phloeidae but does not contribute towards an understanding of the relationships of the family within the Pentatomoidea.

4. The Cydnidae.

The main problems involved in the systematics of this group may be summarised as: (*a*) Is the Cydnidae a homogeneous group or should the Thyreocorinae and Cydninae be raised to higher status, as in Van Duzee (1917) and others? (*b*) What is the status of the group; should it be regarded as a family or should it be included as a subfamily within the Pentatomidae? Most authors are agreed that the Cydnidae ranks as a separate family although some (e.g. McAtee and Malloch, 1933; and Beier, 1938) deny this.

Of the four species examined, two were representatives of the Cydninae and two of the Thyreocorinae. The spermathecae of three of these, *Sehirus*, *Macrocytus* and *Thyreocoris*, are clearly of the same type while the third, that of *Galgupha* (Thyreocorinae), is very different. It is unfortunate that it has not been possible to examine further species from the Thyreocorinae in order to test whether *Galgupha* is aberrant in respect of the spermatheca or whether there is diversity in the form of the organ in this subfamily. However, if one accepts *Thyreocoris* as typical of the Thyreocorinae, then it can be stated that the evidence suggests that the Cydninae and Thyreocorinae should be regarded only as subfamilies of the Cydnidae.

In regard to the status of the family, evidence from the reproductive organs is somewhat more helpful. The three spermathecae which are similar have a large apical bulb, a prominent pump region with wide flanges, and a duct whose basal parts are modified by partial invagination to form a complex, dilated region. The form of this differs slightly in the three species, the cuticular parts being somewhat more fused in *Sehirus* and *Macrocytus* than in *Thyreocoris*. In all cases it is evident that this structure is of the same type as that found in the Pentatominae (and some other subfamilies of the Pentatomidae) but the modification of the duct in the Cydnidae is of a lesser degree.

The bulbus and associated glands of the male reproductive organs of *Sehirus* are very complex, probably even more so than those of the Pentatominae. They are, nevertheless, of the same type, ectadenes and an ectodermal sac being present.

To sum up this evidence on the question of the status of the Cydnidae, it can be stated that, in the form of the spermatheca and the male reproductive organs, affinities with the Pentatominae are indicated. However, the differences seem to be of sufficient degree to suggest (when considering these characters only) family status for the group.

5. The Pentatomidae.

There is little agreement amongst authors on the status of the groups to be considered below. Such is the disagreement that in some cases it is a question

of considering whether a group should have tribal, subfamily, or even family status.

Pentatominae.

The spermathecae and male reproductive organs of several species of this group have been examined and their form found to be very constant.

The spermatheca is characterised by a complex dilation which extends over most of the length of the spermathecal duct. This is formed by the invagination of the apical within the more proximal parts of the duct. The male reproductive organs are also distinctive. The bulbus ejaculatorius is very complex and provided with tubular ectadenes and an ectodermal sac or sacs.

It is not intended to discuss the status of the group at this point. Some other subfamilies have very similar reproductive organs and discussion is deferred until these have been considered.

Graphosomatinae, Asopinae, Discocephalinae, Phyllocephalinae.

The spermathecae of these groups have the same features as those of the Pentatominae. The male reproductive organs of the Graphosomatinae are of the same type as those of the Pentatominae.

The spermathecae of the remaining subfamilies which have been examined differ considerably from those of the five groups noted above. Because of the uniformity in the spermathecae and in the male reproductive organs (where these have been examined), it is suggested that the five groups Pentatominae, Graphosomatinae, Asopinae, Discocephalinae and Phyllocephalinae might be regarded as constituting a group somewhat removed from the other subfamilies. Such a system would involve either the lowering of the status of these five related groups to tribal level, or raising that of the remaining subfamilies to family level. This will be discussed at the end of the section. Unfortunately, the amount of published information on the comparative morphology of the groups is small, so that until other studies have been carried out it will be difficult to assess with certainty the value of the conclusions reached here. As far as can be ascertained from the literature on the wing venation (Kirkaldy, 1909), the form of the egg and the egg burster (Esselbaugh, 1946; Miller, 1934; Heymons, 1906; Kobayashi, 1951; Leston, 1953*a*) and the male genitalia (Singh-Pruthi, 1925), they form a distinct group. It is of interest that Singh-Pruthi included in his Pentatominae group only the five subfamilies under consideration here. Leston (1953*a*), in defining in detail the Podopinae (for a discussion on the nomenclature of this group see Leston 1953*a* and *b*), has shown that there is evidence of close relationship between this group and the Pentatominae. While claiming subfamily status for it, he has noted that it differs from the Pentatominae so slightly that it is probable that subsequent research will lead to a drop in its rank.

Scutellerinae.

Although it is usually placed as a subfamily of the Pentatomidae, Reuter (1912) regarded this group as of family status, a practice followed by Van Duzee (1917). Reuter remarked that the Scutelleridae differ without doubt as much from the other Pentatomidae as do the Urolabidae. Kirkaldy (1909),

while keeping the group as a subfamily, showed that they are separated from the Pentatominae, Phyllocephalinae, and Asopinae in the venation of the wing. Singh-Pruthi (1925) noted that there is a scutellerine type of male genitalia. Leston (1954), from studies on the wing venation and aedeagus, placed the Scutellerinae, Tessaratominae and Phloeidae apart from the Pentatominae. However, he found that in the characters of the eighth male segment and second abdominal spiracle the Scutellerinae showed similarities with the Pentatominae.

The male reproductive organs are similar to those of the Pentatominae. They differ only in the absence of ectodermal sacs. The spermathecae, however, show no affinity with those of the Pentatominae. They are of the pentatomoid type but differ from those of the Pentatominae in the form of the spermathecal duct. Most of the spermathecae of Scutellerinae examined are characterised by a long, tubular apical bulb, a long pump region, and especially by a very large, ovoid or spherical heavily sclerotised and deeply pigmented dilation of the spermathecal duct. This dilation is not formed by invagination, as is that in the Pentatominae. One spermatheca did not have this form, the duct being thin-walled and the dilation saccular and unsclerotised.

Thus, on the character of the spermathecae, it is suggested that the Scutellerinae might rank as a group separate from that of the five subfamilies with the Pentatominae type of spermatheca.

Dinidorinae.

Kirkaldy (1909) separated the Dinidorinae from the other subfamilies on the venation of the wing. Miller (1934) shows that the eggs and egg-burster differ from those of the Pentatominae. Singh-Pruthi classified the male genitalia as of the tessaratomine type. Leston (1954) has shown that this is not the case.

The spermatheca of the species examined by the writer is unique and, except for having a pentatomoid pump region, shows no similarities with those of other groups. It is large and lined with a very thick, firm cuticle. It has a short, wide duct which bears a very long, wide, tubular diverticulum.

Thus the evidence from the spermatheca confirms the independent status which the group is usually given.

Tessaratominae.

It is generally agreed that this group merits subfamily status, although Dupuis (1953), without giving his reasons, has regarded it as a family. Kirkaldy separates it from the other subfamilies on the character of the exposed second abdominal spiracle. Leston (1953*c* and 1954) has shown that, as in *Phloea*, the eighth segment is large and complete and its spiracles are large and functional (in contrast to the condition in the Pentatominae). He also notes that the wings, like those of the Phloeidae, show certain characters, which he regards as primitive. The eggs described by Miller differ from the Pentatominae type, as does the egg-burster.

Except in the case of the one species (a member of the tribe Oncomerini) the spermathecae examined (from the tribes Eusthenini, Natalicolini and Tessaratomini) have a common pattern. The main features are an ovoid or

spherical bulb, prominent pump region and a duct which has an ovoid, sclerotised dilation whose chitinous lining is sculptured in a characteristic fashion. Basally the duct is wide and the lining marked with annular thickenings. The vaginal intima at the point of entry of the duct bears massive sclerotisations. In the species from the Oncomerini the duct has an apically-placed saccular diverticulum.

The character of the spermatheca, therefore, would suggest that the Tessaratominae should be regarded as an independent group and with a status equal to, for example, the Scutellerinae.

Acanthosominae.

This group has been given, by different authors, the status of tribe, subfamily and family. The general opinion of systematists is that it should have subfamily rank within the Pentatomidae. However, Kirkaldy (1909) treated the group merely as a tribe. Dupuis (1948) raised the group to family rank, but as this was done in a footnote to a paper on heteropteran parasites, few reasons are given. Recently Leston (1953*d*) has considered a range of characters and is of the opinion that it merits family status. In addition to the two segmented tarsi, the ventral spine and the carinate mesosternum (not all possess the last two characters), there are other characters which help to distinguish the group. These are: the aedeagus (distinct from the Pentatomine type) (Singh-Pruthi, 1925, and Leston, 1953*d*); the complete eighth segment in the male (Baker, 1931); the egg (without a cap, tubercles, egg-burster and with longitudinal splitting on hatching) (Myers 1926, MacGill, 1942); the abdominal setose organs (Pendergrast, 1953); and the bacteria-smearing organs of the female (Rosenkranz, 1939; Pendergrast, 1952; Carayon, 1952*e*).

The male reproductive organs differ from those examined in all other groups of the Pentatomoidea. Mesadenes are present, but there are no ectadenes or ectodermal sacs associated with the bulbus. Thus, they are similar to the organs found in many other Trichophora (outside the Pentatomoidea) and especially those of the Pyrrhocoridae. The spermatheca is simple also. There is an apical bulb, a pentatomoid type of pump region and a duct with a swollen spirally-twisted base.

Therefore, this evidence suggests that the group merits status higher than that of a tribe of the Pentatominae. The simple reproductive organs would also suggest some affinities with Trichophora outside the Pentatomoidea. This would support Dupuis' opinion that the group is primitive, an opinion with which Leston (1953*d*) does not agree.

6. The status of the groups of the Pentatomoidea.

Amongst the diversity of types of reproductive organs in this superfamily there are certain groups in which the spermathecae and male reproductive organs (where they have been examined) are all of the same type (Pentatominae, Asopinae, Graphosomatinae, Discocephalinae, Phyllocephalinae). Apart from these there is a collection of families and subfamilies all with characteristic reproductive organs, clearly pentatomoid (except for the Urolabidae), but unlike those of any other group.

Therefore, the suggestion is that, should other evidence bear out this conclusion (as it has in the Acanthosominae), all these groups with the non-Pentatomine type of reproductive organs deserve equal status; e.g. it is considered that the reproductive organs of the subfamily Tessaratominae are as distinct from the Pentatominae as are those of the family Plataspidae. In fact, in the case of the Acanthosominae and the Cydnidae, the organs of the latter group show considerably more affinity with the Pentatominae than do those of the Acanthosominae. The question whether these groups should be of family or subfamily rank is beyond the scope of this study, since it would require an extensive knowledge of the other families of the Trichophora. In any case, however, it is considered that, on the evidence of the spermatheca, the Urolabidae deserve to rank as a separate family.

The conclusions can be illustrated in the following scheme :—

(*a*) Of definite family status :

Urolabidae.

(*b*) A single group consisting of :

Pentatominae.
Asopinae.
Graphosomatinae.
Discocephalinae.
Phyllocephalinae.

(*c*) The remaining groups, each of equal rank with the whole of group (*b*) :

Scutellerinae.
Tessaratominae.
Acanthosominae.
Dinidorinae.
Cydnidae.
Phloeidae.
Plataspidae.

VIII. The Value of the Reproductive Organs in Classification.

The preceding discussion has shown that, when the grouping of the families and subfamilies on the characters of the reproductive organs is compared with the systems of classification of several authorities, agreement is observed in some groups, disagreement in others. It is obvious that no final assessment of the value of the reproductive organs in systematics will be possible until those other characters, on which the usual systems of classification are based, are subjected to detailed investigation throughout the suborder. As it is, the writer would claim that a case has been made out for further investigations of the form of the reproductive organs in many more genera, both in groups where the taxonomy has been intensively studied and in others, such as the Coreidae, where a considerable amount of taxonomic investigation remains to be done.

From the point of view of the taxonomist, the spermatheca is obviously of more use than the male reproductive organs as it can be studied from dried material. Finally, it might be pointed out that even where the spermatheca is shown to be of little value in the systematics of the higher groups, it may possibly be of use at generic level. The study of the organ in fourteen genera of Lygaeidae indicates that this is the case.

IX. The Grouping of the Families on the Evidence of the Reproductive Organs.

A. Hydrocorisae.

Notonectidae, Pleidae, Helotrephidae, Gelastocoridae.
Nepidae, Belostomatidae.
Naucoridae, Aphelocheiridae, Ochteridae, Corixidae.

B. Amphibicorisae.

Gerridae, Hebridae, Hydrometridae, Mesoveliidae, Veliidae.

C. Geocorisae.

Reduviidae, Phymatidae, Tingidae.
Cimicidae, Anthocoridae, Polyctenidae, Microphysidae, Miridae, Nabidae, Velocipedidae.
Saldidae, Leptopodidae, Aëpophilidae.
Coreidae.
Berytidae.
Aradidae.
Pyrrhocoridae.
Pentatomoidea (see conclusion to Part VII).

Geocorisae of uncertain position :—

Lygaeidae, Colobathristidae, Piesmidae, Cryptostemmatidae, Enicocephalidae, Dysodiidae.

X. Summary.

1. The female reproductive organs, especially the spermatheca, have been studied in thirty-five families of Heteroptera. Information from the literature on eight other families has been included.

2. The male reproductive organs from twenty-five families have been described, and further information from the literature on eight other families has been added.

3. The study demonstrated that :

(*a*) In the female, the spermatheca (or when it is absent, the type of fecundation and the form of the bursa copulatrix) are of most interest when considering the bearing on classification ;

(*b*) in the male the characters of interest are the presence or absence of a complex bulbus ejaculatorius, the accessory glands, and the number of testis follicles.

4. The systems of classification of the Heteroptera by several authorities have been examined in the light of evidence from the reproductive organs :

(*a*) To attempt to assess the values of the organs in systematics ;

(*b*) to provide the evidence in a convenient form, should it be required for use without evidence from other characters in future attempts at classifying the Heteroptera.

5. The study suggested that, on reproductive characters :

(*a*) There is a division of the suborder into three major groups (Hydrocorisae, Amphibicorisae, Geocorisae) ;

(*b*) certain families form groups corresponding in large measure with generally accepted superfamilies ; e.g. Cimicoidea, Gerroidea, Pentatomoidea, Notonectoidea. Other groups show little correspondence. Final assessment of the validity of these groups, and of the value of the reproductive organs in systematics, is impossible until other taxonomic characters are subjected to detailed study.

6. The Pentatomoidea was treated at family and subfamily level. The Urolabidae show some affinities outside the Pentatomoidea. Of the other families and subfamilies, some (e.g. Cydnidae, Acanthosominae, Scutellerinae and others) appear to merit equal rank with each other and with the whole of a group including the Pentatominae, Graphosomatinae, Asopinae and others.

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XII. Key to Lettering of Figures.

Figures 1–71 (Female organs).

ag, accessory gland.
at, apical tube of the spermatheca.
av, aperture opening from the spermatheca into the vagina.
b, spermathecal bulb.
co, common oviduct.
d, spermathecal duct.
dd, distal part of spermathecal duct.
dl, dilated portion of spermathecal duct.
dp, proximal part of spermathecal duct.
ds, sac-like outgrowth of spermathecal duct.
e, egg.
ep, epithelium.
f, funnel-like ducteole.
fc, fecundation canal.
fd, distal flange of pump.
fl, flange of pump.
fp, proximal flange of pump.
g, secretory cells or secretory cell layer.
i, cuticular intima.
m, muscle.
o, lateral oviduct.
op, ovipositor.
p, spermathecal pump.
r, rectum.
s, spermatozoa.
sc, sclerotised muscle attachment.
sl, sculpturing of the cuticle.
sp, spermatheca.
st, region responsible for the storage of sperm.
t, thickening of vaginal intima.
v, vagina or vaginal wall.
ve, vaginal epithelium.
vi, vaginal intima.
vp, vaginal pouch (" Vaginaltasche " of Larsén).
z, intermediate part of the spermatheca, or " Zwischenstück " of Larsén.

Figures 72–122 (Male organs).

b, bulbus ejaculatorius.
d, ductus ejaculatorius.
eg, ectadene accessory gland.
ep, epithelium.
ep_1, outer epithelium of the bulbus ejaculatorius. This is continuous with the epithelium of the ductus ejaculatorius.
ep_2, epithelium within ep_1 which partially or completely surrounds ep_3.
ep_3, epithelium lining the lumen of the bulbus.
er, reservoir of the ectadene gland.
es, sac of ectodermal origin. Epithelium is continuous with ep_1 of the bulbus.
g, accessory gland.
gd, duct of accessory gland.
i, cuticular intima.
m, muscle.
mg, mesadene accessory gland.
mg_1, paired glands.
mg_2, unpaired glands.
mr, mesadene reservoir.
pg, pygophor.
pm, peritoneal membrane.
s, sperm.
se, secretion.
se_1, dense compacted layer of secretion, often refractile and having the appearance of a cuticular layer.
t, testis.
$t_{1, 2}$, etc., testis lobes.
v, vas deferens.
ve, vas efferens.
vg, glandular portion of vas deferens.
vs, vesicula seminalis.